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CONSERVATION GENETICS: THEORY AND PRACTICE[1]

Barbara A. Schaal[2] *and*
Wesley J. Leverich[3]

Abstract

Conservation biology is a broad field that overlaps many areas of biology including environmental science, ecology, molecular biology, population genetics, and evolution. Included in conservation biology is a range of activities, from theoretical studies to on-site management of endangered species. One of the challenges for conservation biology is to relate the processes that are of interest for research scientists to the practical application of these issues by conservation managers. Field biologists are faced with the dilemma of reconciling processes that on a theoretical level could be of concern for conservation efforts with the subset of processes that will actually have an effect on plants in the field. Here we examine some of the dysgenic consequences of small population size that could potentially affect the success of conservation and restoration efforts, including loss of genetic diversity, genetic drift, and inbreeding and outbreeding depression. There are examples in the literature which demonstrate that all of these population genetic processes can negatively affect plant fitness. In many cases the magnitude of these negative effects is relatively small. We use Wallace's concept of hard and soft selection to suggest that the reproductive excess of plant populations can, in some cases, accommodate such small losses of fitness and provide flexibility for conservation managers.

Key words: conservation genetics, genetic drift, inbreeding depression, outbreeding depression.

Conservation genetics is a broad field with many different areas, ranging from the phenotypic effects of inbreeding to the use of genetic markers for identity. Frankham (1995) divides conservation genetics into three areas: the genetic management of small populations, resolution of taxonomic status of conservation units, and the use of genetic markers, such as in forensics. For this discussion we are going to be concerned with the first: the genetics of small populations (Ellstrand & Elam, 1993). Included are such topics as loss of genetic diversity, genetic drift, inbreeding and outbreeding depression, adaptation to captivity, and the accumulation of deleterious mutations.

One of the challenges for conservation biology is the disparity between the processes that are of interest to population geneticists and the practical application of these issues by conservation managers. Population geneticists worry about such things as inbreeding depression and the movement of genotypes from one geographical provenance to another. And, there is an increasingly large body

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[2] Department of Biology, Washington University, St. Louis, Missouri 63130, U.S.A. schaal@wustl.edu
[3] Department of Biology, St. Louis University, St. Louis, Missouri 63103, U.S.A. leverich@slu.edu

of work that relates genetic issues to the long-term success of populations (Soulé, 1986; Fenster & Dudash, 1994; Montalvo et al., 1997; Lande, 1999; Krakowski et al., 2003). But how much do these academic issues bear on the real, on-site practice of conservation biology? Field conservation biologists are often faced with the dilemma of reconciling processes that, on a theoretical level, could be of concern for conservation efforts with the subsets of processes that will actually have an effect on plants in the field. To illustrate the problem, early "common-garden" studies of plant local adaptation have led to the notion that plant populations are very precisely adapted to local habitat and that moving genotypes to different environments will cause a loss of adaptation (e.g., the studies of Clausen et al., 1940, 1948). These early findings have resulted in some field practitioners being reluctant to move plant genotypes across very small distances in an effort maximize local adaptation and to keep local gene pools "pure." In some cases restoration efforts have been abandoned because no local plant seed sources are available. On the other end of the spectrum, several plant population geneticists have questioned whether the issues studied by population geneticists have any real bearing on field practices whatsoever. "Conservation genetics studies are worthless; you should take the money spent on genetic studies and buy land and fences—that will do the most good" (Anonymous, pers. comm.).

Many practicing conservation biologists are justly concerned about the processes identified in academic population genetics studies and worry that their own conservation efforts will be ineffective due to some process that is currently only of academic interest. Conservation biologists have little guidance on how to actually deal with such genetic issues when they are confronted with them in the field (but see Hufford & Mazer, 2003). Do theoretical population genetics issues matter? Do they affect practical conservation efforts, or are they only of academic interest? These are difficult issues to resolve, and clearly all processes that potentially *could* affect field populations in reality do not. Below we examine some of the dysgenic consequences of small populations that could potentially affect the success of conservation and restoration efforts and, hopefully, provide some guidance for conservation efforts in the field.

Loss of Genetic Diversity

One of the expected consequences of habitat loss and fragmentation is a reduction in population size and, consequently, a loss of genetic diversity (e.g., Jain, 1994; Young et al., 1996; Smith et al., 2003). Does the loss of genetic diversity increase the likelihood of extinction? There are some clear examples where this is the case. Over half of all flowering plants are self-incompatible. If population size is extremely small, populations will have reduced levels of genetic variability at all loci, including the self-incompatibility (S) locus. There is the possibility of a small population becoming fixed for one S allele, which results in individuals no longer being able to reproduce. Such loss of S allele diversity and consequently the ability to sexually reproduce has been observed in several species (*Hymenoxys acaulis* (Pursh) K. L. Parker (Demauro, 1993), *Aster furcatus* E. S. Burgess (Les et al., 1991; Reinartz & Les, 1994), *Rutidosis leptorrhynchoides* F. Muell. (Young et al., 2000), *Asclepias meadii* Torrey (Hayworth et al., 2002), and *Cochlearia bavarica* Vogt (Fischer et al., 2003)). Even without self-incompatibility alleles, loss of genetic diversity can increase the probability of extinction. In a study of *Clarkia pulchella* Pursh, populations that had low diversity suffered 75% extinction in three generations, whereas populations with high diversity had a much lower rate of extinction, 21% (Newman & Pilsen, 1997). These and other studies (Reed et al., 2003) suggest loss of variation has long-term negative consequences for some species, but the data can often be contrary. A study of the plant *Lychnis viscaria* L. found no correlation between genetic diversity and fitness components (Lammi et al., 1999). On the other hand, a strong association between genetic diversity and fitness is observed in eelgrass (Williams, 2001). In part these contrary results may be due to such factors as different effective population sizes or inbreeding.

Many of the plants in these studies are normally outbreeders. As population size is constrained, inbreeding with an associated loss of fitness is expected, along with a loss of genetic variation (DeMauro, 1993; Remington & O'Mally, 2000). But plants have variable breeding systems and some habitual inbreeders may suffer few consequences from loss of variation (Beyers & Waller, 1999; Cruzan, 2001). Moreover, many (but not all) population genetic studies are conducted in experimental populations, often removed from normal field conditions that include competition, herbivory, disease, and environmental stress. The question remains, even if loss of diversity can result in increased risk of extinction, how important is loss of diversity relative to other non-genetic processes? Under what field conditions does extinction probability increase? And, can some loss of variability be accommodated in field populations?

Table 1. Clonal structure and variation in RAPD markers in *Asclepias meadii*.

Population	Management	# Plants (shoots)	# Variable markers	# Clones
Douglas, Kansas	Mowed	53	11	3
Barton, Missouri	Mowed	31	9	3
Jefferson, Kansas	Mowed	38	4	3
Franklin, Kansas	Mowed	6	10	2
Anderson, Kansas	Mowed	34	11	10
Leavenworth, Kansas	Mowed	3	0	1
Bourbon, Kansas	Mowed	83	10	5
Miami, Kansas	Mowed	3	3	3
Dade, Missouri	Burned	24	12	10
Jefferson, Kansas	Burned	90	15	21
Saline, Illinois	Burned	16	9	5
Iron, Missouri	Burned	58	10	11

Source: Hayworth et al. (2002).

Genetic Drift

Another genetic issue that is of concern to conservation biologists is habitat fragmentation that results in genetic isolation of populations that were once connected by gene flow. As habitats are fragmented, populations become both demographically and genetically isolated (Giddon & Goudet, 1994; Ellstrand, 1992). Small isolated populations are subject to genetic drift, where genetic changes in allele frequencies can occur at random due to small numbers of individuals (random sampling). Genetic drift is expected to decrease the amount of genetic variation within populations and at the same time increase the genetic variance among populations (Ewens, 1979). When populations of a species become isolated and are reduced in population size, each population undergoes independent genetic drift; the populations will undergo random changes in gene frequency and become more dissimilar, simply by random processes. Is there evidence for random genetic drift in plant species that have experienced habitat fragmentation?

Marlin Bowles and colleagues (Bowles et al., 1998; Hayworth et al., 2002) have extensively studied populations of the threatened species, Mead's milkweed, *Asclepias meadii*. Mead's milkweed is a self-incompatible species that occurs in tall grass prairies of the Midwest. Like many formerly widespread prairie species, it is now confined to isolated prairie remnants with only a few remaining populations in Iowa, Missouri, Illinois, and Kansas. Remaining populations are managed either by mowing or by burning. The choice of management practice has a profound effect on the demography and genetics of populations (Betz, 1989). Populations that are mown have little to no sexual reproduction, since mowing occurs before seed set; reproduction in these populations is primarily asexual with no new genotypes entering the population. Burning is done well after seed set; populations managed by burning reproduce sexually, and thus new genotypes can be recruited into the population.

Studies of genetic variation with populations of *A. meadii* using RAPD (randomly amplified polymorphic DNA) markers have quantified the amount of variation within populations and have estimated the number of distinct clones, that is the number of genetic individuals or genotypes (Table 1). Populations vary in the number of plants, in the number of clones, and in levels of variation. In general, the mown, predominantly asexually reproducing populations have fewer clones (mean 3.75), and less variation (7.25 variable markers) than do the burned, sexually reproducing populations ($x = 11.75$ clones per population; $x = 11.5$ fragments per population) (Table 2). The loss of variation in mown populations appears to be a drift-like process. Since no new genotypes are added to the population because sexual reproduction cannot occur, the only change can be a reduction in the number of clones by either selective or random elimination.

Table 2. Genetic effects of habitat fragmentation in *Asclepias meadii*.

	*Mean number of clones	*Mean number of variable fragments within pops.	*Variance of mean variable fragment no. among pops.
Mown	3.75	7.25	19.6
Burned	11.75	11.5	5.25

* = $P < 0.05$.
Source: Hayworth et al. (2002).

Mown populations conform to the theoretical expectations of genetic drift within populations; the number of clones and the amount of variation is reduced compared to the sexually reproducing populations. Moreover, *A. meadii* populations conform to the second prediction of genetic drift, increased variance among populations. Populations of mown *A. meadii* have a greater variance of mean fragments among populations (19.6) than do the sexually reproducing populations (5.25) (Table 2). These results again suggest that a random, drift-like process is occurring in some milkweed populations. This process is only analogous to genetic drift, because the change in variability is the result of random removal of genotypes, rather than the random addition of genotypes.

Another aspect of genetic drift needs to be mentioned. When effective population sizes are small, genetic drift can overcome the effects of selection on gene frequencies. With small population size and inbreeding, deleterious alleles that would usually be eliminated by selection can not only persist in a population, but also actually increase in frequency (Lynch et al., 1995; Lande, 1995; Beyers, 1998; Whittlock, 2000; Poon & Otto, 2000). Experimental evidence from *Gentianella germanica* (Wild.) Boerner indicates that population size is an important factor for the accumulation of mutations within existing plant populations and that small population size increases the chance of extinction due to both the accumulation and increase in frequency of mutations (Paland & Schmid, 2003).

Many experimental conservation genetic studies use genetic markers to infer the levels of genetic variation within populations. It is appropriate to ask whether genetic markers such as allozymes, RAPDs, AFLPs, or microsatellites are good reflections of genetic variation within populations. We have demonstrated above that genetic variation can be critical to the persistence of a plant population. But, persistence is a function of fitness. Fitness, in turn, is affected by variation in quantitative loci (Frankham, 1999). Are molecular markers good indicators of variation in quantitative loci? In an important study Reed and Frankham (2001) examined 71 data sets that had both molecular and quantitative measures of genetic variation. They found that correlation coefficients between molecular variation and quantitative measures of variation ranged from negative (−0.88) to positive (0.9) with a mean of $r = 0.217$. This study presents a note of caution in using molecular markers as a proxy for the genetic variation that is relevant for conservation issues. In fact, it is hardly surprising that neutral genetic markers and variation at selected loci show little correlation, since their evolutionary dynamics are governed by different processes, e.g., drift versus selection.

The above considerations suggest that in many cases a decrease in population size and an increase in isolation can lead to reduced variation and to genetic changes that reduce the ability of a population to adapt. Both of these processes, loss of diversity and genetic drift, are tied to each other and can lead to a change in both the number and the types of alleles in a population. These genetic changes can seriously threaten the long-term viability of populations, as the *Clarkia* study illustrates. To manage such situations, where population size is small and diversity is either actively or potentially being reduced, the most reasonable management technique is to either prevent such genetic erosion before it occurs or to counter the loss of variation. Since alleles are being lost, the most straightforward method of management is to introduce new alleles by migration, or the artificial introduction of alleles from different populations. One may argue that this disrupts the genetic "purity" of a population and could introduce maladapted genotypes. But, it seems to us that when a given population is threatened with a high prospect of extinction, there are only two choices: let the population go extinct, or add new alleles in an attempt to counter the loss of genetic variation. It is difficult to imagine scenarios where extinction is preferred over the addition of new alleles.

Outbreeding Depression

One of the most vexing issues for practicing conservation biologists deals with the source of seeds or plants for conservation efforts (the geographical provenance of plants or, in the terminology above, the source of migrants for reintroduction). Does mixing genotypes from different geographical regions result in a loss of fitness? Such potential loss of fitness might result from combining disparate genomes that are adapted to different environments (Primack, 1996; see Dudash et al., 2005 this issue). This loss of fitness may be due to crossing plants from geographically distinct regions, or it may possibly occur even among the plants of a single structured population. Issues of outbreeding depression are a major concern for both the management of small in situ populations and for restoration work. Recent studies have developed the concept of "seed transfer zones" that define a geographical region within which seeds can be collected with little probability of incurring dysgenic effects (Hufford & Mazer, 2003).

Table 3. Flowering date for *Bouteloua gracilis* in a common garden.

Transplant source location	Flowering date
Manitoba	May 21
North Dakota	May 21
N Nebraska	May 25
S Nebraska	June 6
Colorado	June 12
Kansas	July 3
Oklahoma	Aug. 14
Texas	Aug. 24

Source: McMillan (1964).

Much of the concern for harm resulting from migrants comes from conclusions of common-garden transplant experiments. Early studies by Clausen et al. (1940, 1948) used common-garden experiments to determine genetic differentiation between ecotypes of a species. These studies often used clonal replicates of field-grown plants, and they have shown strong local adaptation in reproduction and survivorship. These results suggest that the source of plants or seeds might have a strong effect on survivorship and fecundity of introduced plants at a given location. Moreover, introducing migrants from other populations may introduce alleles that are maladaptive to the local environment. Given the importance of these studies for conservation biology, we examine transplant studies in more detail.

One of the most detailed series of studies on ecotypic differentiation was conducted by Calvin McMillan and his students at the University of Texas (McMillan, 1964, 1969). They examined local adaptation and ecotypic differentiation across a latitudinal and elevation gradient in prairie grasses, determining geographical differences in flowering time, morphology, and physiology. Their results showed that transplant survival could decrease as the geographical distance between source population and transplant site increases. Their results also demonstrated that grass species show differences in the degree of geographical differentiation. Table 3 shows typical results for the first flowering date of *Bouteloua gracilis* Lag. ex Griffiths, in a common garden in Texas for plants collected between Manitoba and Texas. First flowering date varies over a three-month period from May 21 for plants from Manitoba to August 24 for Texas-collected plants. Table 4 shows geographical variation in survival of plants transplanted to Texas. In some cases plants collected from geographically removed areas could not survive at all at the Texas site; all three species collected from North Dakota did not survive transplantation. These results justifiably cause alarm for conservation biologists, indicating that transplants from geographically remote regions will not flourish.

Do plants that are collected within the same geographical region show similar levels of local adaptation? Zampini (1991) conducted an experimental study of survivorship and reproduction among an identical set of *Helianthus tuberosus* L. clones. She replicated genotypes from four field sites within the greater St. Louis region, and then transplanted plants from all of the sites back into the four initial field sites. Table 5 shows that both survivorship and fecundity is highly variable among sites. Based on an analysis of variance, differences in survivorship and fecundity had no statistical genotypic association in this experiment; rather the variance of fit-

Table 5. Survivorship and reproduction in an identical set of *Helianthus tuberosus* clones: effect of the environment.

Transplant site	Survivorship to day 200	Reproduction (no. of ramets)
1	54%	3.27
2	44%	1.39
3	97%	25.42
4	58%	1.12

Source: Zampini (1991).

Table 4. Survival of clones transplanted to Texas: effect of genotype.

	Number surviving (number transplanted)			
Transplant source	*Andropogon scoparius* Michx.	*Andropogon gerardii* Vitman	*Panicum virgatum* L.	*Sorghastrum nutans* (Nash) Hitchc.
North Dakota	0 (12)	0 (12)	0 (6)	—
Nebraska	2 (12)	0 (12)	11 (12)	0 (11)
Texas	12 (12)	12 (12)	12 (12)	12 (12)
Arizona	0 (10)	6 (6)	0 (12)	11 (12)
Mexico	—	0 (5)	0 (9)	0 (11)

Source: McMillan (1969).

ness was associated with the environment of the field site (Zampini, 1991). Plants responded strongly to novel environments by phenotypic plasticity. Additional experiments revealed that variation in quantitative traits associated with fitness was, as expected, related to both genetics and the environment, and to their interaction. In *Helianthus*, many fitness components were more strongly affected by environmental variation than genetic variation. Genetic effects on fitness were only manifest when plants were placed under stress conditions. A comparison of the studies of McMillan and Zampini indicates both a role for genetics and environment in determining fitness (Schlichting, 1986; Scheiner, 1993). These studies suggest a greater role for phenotypic plasticity in fitness when populations are within the same regions. Moreover, a recent study of phenotypic plasticity of plants from large and small populations of *Cochlearia bavarica* Vogt also found little genotypic contribution to phenotypic plasticity in fitness, but did detect an interaction between population size and population identity (Paschke et al., 2003). On the other hand, genetic differentiation is clearly demonstrated across large geographical provenances and in some cases may occur over very short distances, within meters (Antonovics & Bradshaw, 1970).

Another aspect of common-garden studies needs to be mentioned. Common-garden studies transplant adult individuals, often clones. The population dynamics of transplanted adults are very different than if seeds were sown into a site. Transplant studies represent well-established genotypes that presumably have been winnowed by selection at their site of origin and should represent a selected subset of the genotypes initially found with an area. Seeds are the result of the meiotic shuffling of genes and due to recombination and independent assortment; they represent a wide array of genotypes, yet unmodified by selection in the field. Thus one might expect that field-collected plants would be more precisely adapted to their environment and represent a more narrow range of phenotypes than would a seed crop from the very same plants. In addition, simply measuring the fitness of a single generation may miss some fitness consequences. While a transplanted genotype may show no loss of fitness in a new environment, the first or second generation hybrids between the transplanted individual and local genotypes may have reduced fitness, e.g., hybrid or F_2 breakdown.

There is one other source of information that bears on the degree of adaptation of plant populations and hence on the fate of introduced germplasm. We can get an idea of how genetically differentiated the populations of a species are based on the population structure of a species and the apportionment of genetic diversity within and among populations (e.g., Hamrick et al., 1991). In many species, both plants and animals, much of the diversity contained within a species is due to the differences among individuals within a population. That is, much of the variation of a species is represented within individual populations. On the other hand, differences among populations can typically account from 5% to 50% of the variation within species (Hamrick & Godt, 1990). The importance of geographical provenance diminishes as the relative diversity within populations increases. Studies of the genetic structure of plant species often report F_{st} values; F_{st} is an indication of the degree of genetic differences among populations and is measured by the variance in allele frequencies across populations. Low F_{st} values indicated that there is little genetic differentiation among populations. Species that are highly variable with little differentiation among populations will show fewer effects of mixing remote seed sources than those that have highly differentiated local populations. Table 6 shows the levels of apportionment of genetic variation within and among populations of two glade species in Missouri, *Clematis fremontii* S. Watson (Learn & Schaal, 1987) and *Rudbeckia missouriensis* Engelm. (King & Schaal, 1989). Both species are outcrossing perennials and grow on isolated glade sites, yet they have very different genetic structures. *Rudbeckia* shows little genetic differentiation among populations, with $F_{st} = 0.11$, whereas *Clematis* has F_{st} values for different glade populations of 0.36. Overall, *Clematis* has much more diversity, but it is allocated among different populations. *Rudbeckia* has less diversity but it is shared across populations. *A priori* one expects that *Rudbeckia* would be much more tolerant of mixing genotypes of different populations than would be *Clematis*, which has many more genetic differences among populations. This comparison of population structure suggests that the importance of geographical provenance for conservation work will vary among species. We can use studies of genetic var-

Table 6. Population structure in glade plants.

Within populations	F_{is}	F_{st}	H
C. fremontii	0.22	0.16	0.56
R. missouriensis	0.01	0.03	0.09
Among populations	F_{is}	F_{st}	H
C. fremontii	—	0.36	1.2
R. missouriensis	—	0.11	0.21

Source: Learn & Schaal (1987); King & Schaal (1989).

Table 7. Inbreeding depression in *Lupinus texensis*.

	Selfed	Outcrossed	Reduction in fitness
# leaves at 6 weeks	20.78	23.43	11.2%
# flowers	88.4	108.6	18.2%

Source: Schaal (1989).

iation and population structure to access the potential dysgenic effects that might occur if genotypes of different populations are mixed in restoration or conservation efforts.

What can we conclude about geographical provenance? Transplant studies indicate that across broad geographical ranges, strong adaptation to regional geographical provenance can occur. On a more local scale, within a region, the levels of local adaptation are variable. In many cases phenotypic plasticity is an alternative to local genetic adaptation at least for some species. Studies of population structure, which examine the distribution of genetic variation, can be used to access potential effects of mixing genotypes from different populations and are an important tool for conservation and restoration work. Finally, the effects of seed introduction are different than adult transplants and one needs to interpret the results of common-garden experiments with caution.

Inbreeding Depression

Another important dysgenic effect that can occur in species with small population size is inbreeding depression. As populations of outcrossed species become reduced in size, crossing will eventually occur among genetically related individuals, increasing the level of inbreeding. Inbreeding increases the level of homozygosity in a population, which can in turn have a negative effect on fitness (e.g., Frankham, 1995; Frankham & Ralls, 1998; Hedrick & Kalinowski, 2000; Day et al., 2003). This is a well-documented phenomenon in plants, both in domesticated crops and in native species (e.g., Fenster & Galloway, 2000; Sheridan & Karowe, 2000; Remington & O'Malley, 2000; Krakowski et al., 2003). Table 7 shows typical results for an outcrossing plant species, in this case, *Lupinus texensis* Hook., an annual plant with large populations. The species can self, but is usually outcrossed. When selfed it experiences varying levels of inbreeding depression (some populations show strong inbreeding depression while others show relatively little effect). Table 7 shows the effect of inbreeding depression for a population of *L. texensis*. Plants that are the product of selfing are smaller at six weeks (they have fewer leaves), and they also have fewer flowers compared with outcrossed progeny. These differences correspond to a reduction in fitness of 11.2% for size and 18.2% for number of flowers.

Table 8. Genetic effects of inbreeding or outbreeding depression (hypothetical illustration).

Loss of fitness (death or maladaptation)	5%	10%	20%	50%
Number of seeds planted	Resulting population size			
10	9.5	9	8	5
100	95	90	80	50
1000	950	900	800	500

Both outbreeding depression and inbreeding depression are processes that generate genotypes of potentially low fitness within a population, but the number of alleles may not be reduced. This is in contrast to the genetic effects associated with reductions in population size, where the number of alleles and their diversity of alleles may be reduced. Inbreeding and outbreeding depression affect genotypic distributions, but not allelic distributions. However, such changes in genotypes can lead to other, relatively less studied issues, such as alterations in the gene by environment and epistatic interactions among alleles (Fenster & Galloway, 2000).

Conservation Genetics in Practice

How do all of these issues relate to conservation genetics in practice? In light of possible dysgenic effects due to mixing of genotypes from different geographical provenances and inbreeding depression, what should plant conservation biologists do? One possible avenue is to examine the nature of selection in populations. Wallace (1968) developed the interesting concept of hard and soft selection, which attempted to incorporate both genetic and demographic aspects of selection. He defined hard selection as selection that results from genetic constraints—e.g., an individual carrying a lethal gene. Soft selection is defined as selection due to a population that reaches the carrying capacity of the environment. As a population fills up all of the "spaces" in a field site, there is no more room for additional plants and they are selectively eliminated, by soft selection. Table 8 shows a hypothetical example of soft selection. As more seeds are produced to fill a fixed population size, the intensity of soft selection increases. We hypothesize that soft selection can be used to ameliorate some of the dysgenic effects of inbreeding and outbreeding dis-

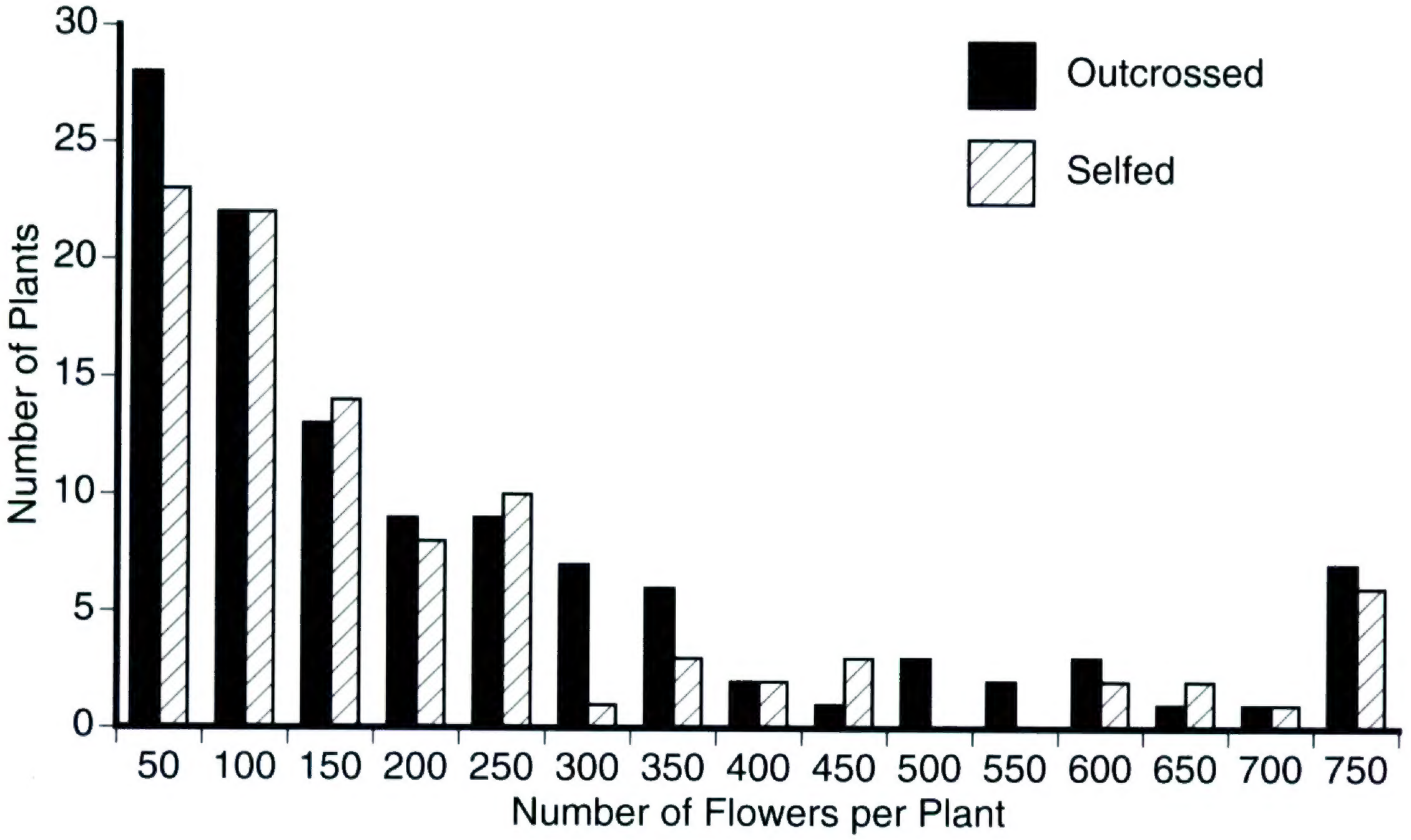

Figure 1. Number of flowers, outcrossed versus selfed. The heights of the bars indicate the numbers of individuals producing the indicated numbers of flowers. Solid bars represent plants grown from outcrossed seed, and hatched bars represent plants grown from self-pollinated seed. (*Lupinus texensis*; from Schaal, 1989; Schaal & Leverich, 2004.)

cussed above (Schaal & Leverich, 2004). Basically, the maladapted seeds produced by inbreeding or outbreeding are included among the seeds that cannot be accommodated in the environment. If there is much excess reproduction, some degree of dysgenic effects can be accommodated. The more individuals produced in excess within the population, the greater is the potential for accommodation of some genotypes with reduced fitness. In fact, this process is seen to some extent in every sexually reproducing plant. Many more seeds are produced than can germinate and reach adulthood. Meiosis produces a range of genotypes with, one assumes, some corresponding distribution of fitnesses. The less fit genotypes are relatively harmless, since most plants have a demographic structure that assures an excess production of offspring as well as a selective sorting of the offspring.

This process would only work if there were adequate numbers of highly fit offspring to replenish a population. To determine if plant populations can tolerate inbreeding and outbreeding depression we need to consider the distribution of fitness as well as the mean reduction in fitness. Figure 1 shows the flower numbers for *Lupinus texensis* plants produced by inbreeding and outbreeding (data from Schaal, 1989). *Lupinus texensis* has a mixed mating system; although natural populations are predominantly outcrossed, they vary in their degree of inbreeding (Helenurm & Schaal, 1996). Both inbreeding and outbreeding produce plants with a range of fitnesses and both produce plants below and above the mean. Even though the mean differences in fitness result in an 18% reduction in flower production and an 11% reduction in the number of leaves, inbreeding produces many plants with very high fitness (Figs. 1, 2). In fact, 45% of selfed progeny have a leaf number greater than the average outbred plant, and 47% have a flower number greater than the average outbred plant. Thus inbreeding, while it affects the mean, still results in the production of many fit individuals, which have the potential to produce completely viable populations. All plants do not manifest inbreeding equally. Some individuals appear to suffer from inbreeding depression while others seem unaffected. If plant populations experience hard and soft selection, some species should be able to tolerate some degree of inbreeding; the loss of fitness should be accommodated in the excess reproduction of populations. And, if outbreeding depression affects the distribution of genotypes in the same way, some levels of outbreeding depression should be accommodated by analogy.

Conclusions

The genetic effects associated with conservation fall into two areas: those that lose allelic diversity

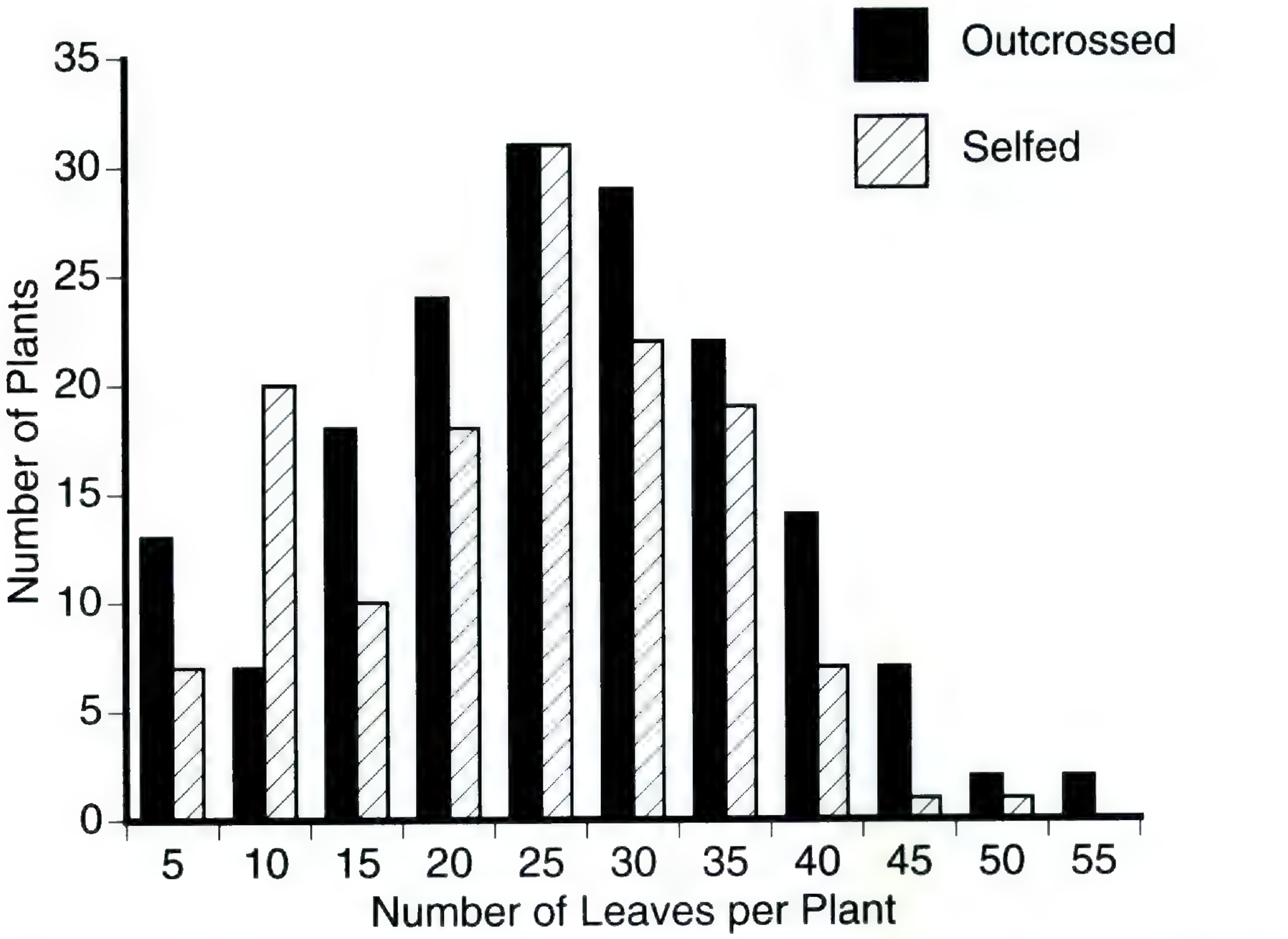

Figure 2. Number of leaves, outcrossed versus selfed. The heights of the bars indicate the numbers of individuals producing the indicated numbers of leaves. Solid bars represent offspring grown from 30 outcrosses, and hatched bars represent offspring grown from 30 self-pollinations. (*Lupinus texensis*; from Schaal, 1989; Schaal & Leverich, 2004.)

(small population size, drift) and those that result in changes in genotypic frequencies (inbreeding, outbreeding). Both processes potentially result in a loss of fitness, but management for these processes differs. The first strategy should be prevention, by maintaining the genetic and ecological processes necessary for viable populations. Unfortunately it is too late for this approach in many species. Threatened plant species often will need direct intervention. In many cases the loss of genetic diversity could be countered by the addition of new genetic variants. Given that extremely small populations are often doomed, such considerations as contamination of the gene pool by non-native alleles seem distant seconds to avoiding extinction.

Population changes associated with the mixing of genotypes from genetically differentiated populations (outbreeding depression) or due to inbreeding can also have large consequences for plant fitness, as has been extensively documented by experimental studies. We argue here that many plant populations may be under soft selection and thus can tolerate some loss of fitness; but this process is limited. If inbreeding or outbreeding effects are severe, then populations will experience demographic instability that can lead to the ultimate demise of the population.

Conservation managers are faced with a series of environmental, ecological, and genetic issues that all can affect the outcome of their efforts to preserve plant species. Many managers worry extensively about genetic issues; these concerns are mostly based on theoretical and experimental academic studies. Field studies of dysgenic effects are increasing, but when empirical data are available, they may be contradictory. We cannot expect every plant species that is of conservation interest to have background data on genetic structure, inbreeding depression, and local differentiation, the data necessary to assess the likelihood of dysgenic effects. Field-based conservation efforts need to be based on a series of principles that will assist when background data are unavailable. As a first principle one would like to maintain the genetic integrity of a population by not adding migrants and by avoiding inbreeding depression, genetic drift, and loss of diversity. But, a plant species frequently comes to the attention of conservation biologists only when its numbers decline; in most cases it is too late to avoid the genetic consequences of reduced popu-

lation size. Given that many plant populations are dramatically declining, it seems impractical to be concerned with theoretical population genetic issues that are currently being debated in the literature. Based on our discussion of hard and soft selection, there may be some flexibility in accommodating inbreeding and genetic migrants. In particular, overconcern about genetic effects needs to be tempered, given the current debate on the overall importance of genetics in relation to the declines in population size due to habitat loss (Holsinger et al., 1999).

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THEORY AND METHODS FOR DIAGNOSING SPECIES AND POPULATIONS IN CONSERVATION[1]

Paul Goldstein,[2,6] *Yael Wyner,*[3,5] *Phaedra Doukakis,*[3,5,7] *Mary G. Egan,*[5] *George Amato,*[4] *Howard Rosenbaum,*[4,5] *and Rob DeSalle*[5]

ABSTRACT

The analysis of genetic data for the purpose of identifying conservation priorities may draw from one or more biological subdisciplines depending on the specific questions at hand. As such the proliferation of different methods for analyzing and interpreting genetic data in such fields as molecular systematics and population genetics has been paralleled in conservation. We explore the respective realms of utility for these fields and approaches by discussing the juxtaposition of analyses of character distributions with more commonly and often casually used tree-based analyses. In so doing, the biological, philosophical, and methodological convergences and conflicts of these frameworks are explicated using empirical examples, as are some of the areas of overlap among and disagreement over phylogenetic species criteria and other alternatives. In the arena of conservation biology, systematics and population genetics complement one another and may facilitate the identification of management units at intraspecific levels, or more properly intra-nominal levels when species boundaries are defined according to the biological species concept. The comparison of these methods heightens the contrast between graphical representation of reciprocal monophyly at traditionally intra-nominal levels and the identification of groupings actually supported by fixed diagnostic characters as prospective conservation tools. Since character fixation is widely regarded as an early stage in the "ontogeny" of species evolution, character-based approaches to delineating management units provide a suitable framework from within which to explore the complementarity of the two major subdisciplines of evolutionary biology and their respective contributions to conservation.

Key words: conservation biology, population genetics, species criteria, systematics.

Land stewards and conservation biologists have realized the relevance of genetic information to conservation initiatives in several contexts, including the evaluation of population viability (Gilpin & Soulé, 1986; Shaffer, 1981; Menges, 2000), the inference of historical relationships (e.g., O'Brien, 1994), the setting of region-wide conservation priorities based on comparative biogeographic data or species delineation analyses (e.g., Peterson & Navarro-Sigüenza, 1999; Hugall et al., 2002), and most fundamentally the identification of biological "units" for protection, be they species or populations (e.g., Moritz, 1994b; Vogler & DeSalle, 1994; Sites & Crandall, 1997; Petit et al., 1998). In this paper we focus on the small but critical subset of conservation biology concerned with the circumscription and management of such groups and a set of related methods for identifying them.

The original and most obvious source of relevance for genetic data to conservation questions, the evaluation of population viability, was expanded upon the surge of interest in molecular systematics, the purview of which includes traditional systematic endeavors such as the description of new species and the analysis of relationships. In the course of this expansion, the distinction between the primary biological subdisciplines of population genetics and systematics has at times been blurred both logically and analytically by the prevalence of genetic data in both. To summarize the issue in what is perhaps an oversimplified way, population geneticists and systematists occasionally vie for methodological primacy in species recognition and the elucidation of phylogenetic relationships, and are often at odds with respect to the vocabularies they use (Avise et al., 1987). Many published debates

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[2] Division of Insects, Field Museum of Natural History, 1400 S. Lake Shore Drive, Chicago, Illinois 60605, U.S.A. pgoldstein@fmnh.org.

[3] Department of Biology, New York University, Washington Square East, New York, New York 10003, U.S.A.

[4] The Wildlife Conservation Society, The Bronx Zoo, Bronx, New York 10458, U.S.A.

[5] Molecular Systematics Laboratory, Division of Invertebrates, American Museum of Natural History, 79th Street at Central Park West, New York, New York 10024, U.S.A.

[6] Current address: Florida Museum of Natural History, McGuire Center for Lepidoptera and Biodiversity, SW 34th St. and Hull Road, Gainesville, Florida 32611, U.S.A.

[7] Current address: Pew Institute for Ocean Science, 126 East 56th Street, New York, New York 10022, U.S.A.

have thus proceeded at cross-purposes. Some continue to do so by virtue of misunderstandings or by relying on volleys of mischaracterizations instead of critical treatment of ideas. Occasionally, published papers comprise a mixture of scholarship, insight, and contention (Berlocher, 1998; Avise, 2001; Shapiro, 2002), but a number of recent papers have begun to identify and address the salient points of disagreement, and several are quite explicit in issuing caveats as to how molecular data are to be interpreted (e.g., Brower, 1999; Templeton, 2001).

However, the academic nuances of these discussions have not carried over to the applied field of conservation genetics, where, arguably, they have the most immediate consequences (Cracraft, 2000). Many of the misinterpretations surrounding concepts and terminology that have been addressed in the systematics and conservation literature (e.g., Luckow, 1995; Goldstein & Brower, 2002) have nevertheless persisted in the wider audience of conservation practitioners, possibly to an extent that threatens the outcome of conservation and restoration efforts. In our experience, many conservationists are too easily tempted to view genetic data in oversimplified ways that mask the original purposes for which they were generated, or as facile solutions trumping potentially more relevant sources of information such as known behavioral or ecological data that more directly dictate conservation decisions. The Heath Hen *Tympanuchus c. cupido* (L.), an extinct gallinaceous bird last observed and studied on Martha's Vineyard Island, Massachusetts (USA), before its demise (Bent, 1932), has recently been the subject of "reintroduction" proposals (Cokinos, 2000; Palkovacs et al., 2004). Its extant relatives, comprising two named subspecies in the Greater Prairie Chicken complex (*T. c. atwatteri* Bendire and *T. c. pinnatus* (Brewster)) occupy open habitats of the Midwestern United States and have been the subject of conservation genetic studies (e.g., Bouzat et al., 1998a, b). But despite significant behavioral and ecological differences between these birds and the extinct heath hen documented for more than 200 years (Gross, 1928), efforts are under way to introduce prairie chickens to Martha's Vineyard Island (Cokinos, 2000). This endeavor, which entails considerable conversion of habitat for extant threatened species, has been justified on the grounds that, regardless of habitat requirements, genetic "closeness" will suffice for prairie chickens to be viewed as "proto-heath hens" that will ultimately evolve into novel versions of the extinct bird (Cokinos, 2000: 186, 190).

At issue in such situations are the sources of confusion stemming from the correspondence (or lack thereof) between delineated management units and formal taxonomic epithets, and thus the degree to which the methods for delineating conservation units may be at odds. The identification of biological groups for purposes of conservation has several requirements, among them a clearly articulated species concept, regardless of whether the units are themselves to be described as formal species with a set of objective criteria for delineating them, and an explicitly chosen suite of methods compatible with the species concept articulated. Also at issue in this example is the notion that genetic data per se are somehow special or necessarily more relevant than first-hand life history information tied to critical habitat. The desirability of a framework for consistently interpreting character data, genetic, morphological, behavioral, and otherwise, is a theme of this paper.

In this paper we focus on the mechanics and implications of using both character- and tree-based approaches to explore the boundaries of species and other biological units, variously articulated as evolutionarily significant units (ESUs) or management units (Ryder, 1986; Moritz, 1994a, b), the most common distinction being one of biological versus practical focus (Moritz, 1994b; Avise, 2000). It is our thesis that the articulation of such boundaries is both fundamental to the description of nature and critical to the pursuit of science-based conservation. After reviewing some salient points of debate, we reiterate formal limits to the utility of both tree- and character-based approaches and explore their ramifications with reference to empirical examples from animal conservation genetics.

Species Criteria

Choosing criteria for species delineations is among the most fundamentally important issues in biology: such criteria impact our classification schemes, which serve as the primary retrieval systems for all biological information, and they impact how we choose to protect and manage our natural resources. Adoption of different species criteria may lead to startlingly different conservation conclusions. From a legislative perspective, our ability to manage resources is further constrained by scientific definitions adopted under various statutes, and the fact that conservation legislation has not kept pace with either systematic or ecological advances is a potentially serious problem (Shapiro, 2002).

Any careful review of the endless debate over species concepts will reveal that it has proceeded largely at cross-purposes. While some authors ar-

ticulate a desire to ensure consistent and defensible criteria useful to both systematics (Nixon & Wheeler, 1990) and conservation (Goldstein et al., 2000), others are interested primarily in understanding the variety of entities in nature exclusive of formal taxonomy (Hendry et al., 2000; Avise & Walker, 2000). As such, different species concepts apply to qualitatively different kinds of entities at potentially different stages of evolution (Harrison, 1998). No species concept or criterion can legitimately be evaluated as superior to any other without first describing the domain of their applicability (Futuyma, 1998: 453). Various logical parameters involved in *articulating* species concepts are reviewed in Goldstein and DeSalle (2000), but most fundamentally it should be recognized that when choosing an appropriate framework for the delineation of species or conservation units, there is a trade-off between the generalizability of a species concept (or more properly a species criterion; de Queiroz, 1998) and the precision with which it addresses the evolutionary mechanisms by which putative species arise. As Harrison (1998) explained, there are many kinds of biological entities classifiable under a plethora of possible criteria: reproductive isolation, proximity of relationship, diagnosability, presumed mechanisms of evolutionary origin and maintenance, etc. Some of these entities correspond to what many biologists would or have called species; others do not. Harrison's (1998: 28) conception of an ontogeny of species concepts (the "life history of a species") ranges from incipient species at the shallow end of the speciation pool, recognizable only by virtue of one or a few simple fixed differences, to the more deeply diverged species that form evolutionarily cohesive units. It remains for biologists and conservationists to reconcile criteria for the recognition, taxonomic description, and protection of biodiversity. Two broadly fundamental sets of questions are:

(1) In which part of the biological spectrum should we concentrate our systematic delineation efforts? Relatedly, is there a logical, practical, or otherwise important asymmetry between the delineation of species as the elemental units of systematics and the study of coalescence or reproductive isolation?

(2) More fundamentally, for what purpose do we describe species? In other words, what primary functions do species names serve?

Perhaps the most fundamental arena for discussion has to do with the primacy of character state distributions versus the evolution of reproductive isolation, the latter often explicitly equated with biological meaningfulness (e.g. Avise, 2000; Shapiro, 2002), in determining "good" species. When population geneticists, indeed most biologists, speak of speciation, they are usually talking about the evolution of reproductive isolation, and it is a frequent argument against character-based diagnoses of species that since they do not address speciation, they are in effect antiquated, or entrenched, or any of a host of other unflattering monikers. For many reasons, among them the fact that the ability to interbreed does not necessarily indicate immediate sister relationship, and the fact that many organisms are asexual or known only from fossils, Mayr's (1963) biological species concept has been widely rejected by those seeking a more generalizable criterion for species delineation consistent with systematic theory and practice (Noor, 2002). The most recent systematic theorists who have been active in addressing the species problem have very pointedly advanced the idea that species delineation, both as an exercise in nomenclature and as a fundamental endeavor of phylogenetics, falls squarely within the sphere of systematics proper (e.g., Wheeler & Cracraft, 1997), and logically precedes studying the evolution of reproductive isolation. For it to be otherwise, the business of systematics would be forever hampered by appeals to unanswered and possibly unanswerable microevolutionary questions. Although the evolution of reproductive isolation, in contrast, may be studied largely independent of formal taxonomy, population geneticists continue to argue for a primary role in characterizing species (e.g., Coyne & Orr, 1988; Coyne et al., 1988).

Of critical interest, then, are the questions of where reproductive isolation and cladogenesis fail to coincide and the degree to which biological groups may be diagnosed below traditional taxonomic boundaries. Once it is recognized that different characterizations of biological entities refer, at least potentially, to different stages in a potential evolutionary progression, there remains only to determine where the formalization of species needs to be concentrated (Prendini, 2001). Such issues are rarely addressed in discussions of species concepts (e.g., Wu, 2001).

At the very least, researchers in the inchoate field of conservation genetics should be familiar with the basic parameters of species concepts and the implications of various analytical criteria and methods with respect to those concepts (Goldstein et al., 2000). There are many species concepts to choose from (for reviews see Otte & Endler, 1989; Templeton, 1989; Cracraft, 1989; Frost & Kluge, 1994; Howard & Berlocher, 1998; Goldstein & DeSalle, 2000) beyond the purview of this paper. Here, we focus on the mechanics of the most widely

used and/or controversial criteria for species identification, the biological (Mayr, 1963), the cohesion (Templeton, 1989), the phylogenetic (sensu Cracraft, 1989), and the genealogical (Baum & Shaw, 1995) species concepts, toward identifying the theoretical and operational issues inherent to the delineation of species and populations for conservation management (see appendices in Goldstein & DeSalle, 2000).

The Biological Species Concept

The biological species concept (BSC) defines species as "groups of actually or potentially interbreeding natural populations that are reproductively isolated from other such groups" (Mayr, 1969: 26). Although the BSC was defined initially with animal biology in mind, Stebbins immediately recognized and applied the BSC to plants, observing its conceptual origin in the work of Dobzhansky, and Mayr (1992) himself much later attempted to illustrate its applicability to botany. Recognizing that this conception is inherently restricted to extant sexually reproducing organisms, the assessment of interbreeding is, moreover, frequently compromised by the very nature of natural populations. Many animal populations for which questions about species boundaries arise are allopatrically distributed, making direct measurement of potential interbreeding an empirically difficult task (Avise & Ball, 1990). Other primary criticisms of the BSC are more recently reviewed in Zink and McKitrick (1995) and Noor (2002) and include the fact that interbreeding is not necessarily an indicator of closest relationship (cf. Rosen, 1979).

Of interest here are the methods that have most recently been brought to bear on the question of delineating biological species. Methods most commonly used as proxies to measure interbreeding and hence evaluate species status include both distance analyses and phylogenetic analyses of sorts. The development of distance measures allowed both allozyme and genetic data to be used as measures of genetic similarity among sibling species, subspecies, and populations (Nei, 1972). Ayala et al. (1974) used *Drosophila* to show that genetic similarity was greater within species than between species. Highton (1989, 1990) and Porter (1990) also elaborated methods for distinguishing species based on distance and gene flow statistics, respectively, both explicitly or otherwise within the framework of the BSC. But other authors have since cautioned against using such approaches by showing that published between-species divergence can be less than that between conspecific populations (see Vogler & DeSalle, 1994, fig. 1). This problem is particularly acute since there can be no objective criterion for delineating a species based on genetic distance.

Another approach to delineating biological species, suggested by Avise and Ball (1990), is to perform phylogenetic analysis on different genetic loci from natural populations. Populations are assessed for reciprocal monophyly (see fig. 3 in Goldstein et al., 2000) and topologies for concordance between different gene regions. If these criteria are met, and if there are no examples of interbreeding populations in the wild, then populations are classified as distinct biological species. If hybrid populations have been observed, then the reciprocally monophyletic populations that gave rise to the hybrid population require special consideration at the nomenclatural level of subspecies (Avise & Ball, 1990).

It is imperative to recognize that the paradigm of intraspecific phylogeography championed by Avise (1994, 2000; Avise & Hamrick, 1996) is tied explicitly to the biological species concept. Given that the phylogenetic species concept (described below) defines a species as that level below which hierarchical representation of relationship is artificial, "intraspecific" phylogenetic reconstruction is by definition much more problematic, if not spurious. To the extent it is used in a phylogeographic context on named entities corresponding to reproductively cohesive biological species, the term "intra-specific" should properly be revised as "intranominal."

The Cohesion Species Concept

Templeton (1989) introduced the cohesion species concept (CSC) based on recognition of two biological observations inherent to the speciation process: (1) a species is an evolutionary lineage, and (2) the species represent reproductive communities. Templeton (1998b) suggested that the more reliant species criteria are upon these universals, the more useful and general the concept becomes. As Templeton (1998b: 33) stated: "The cohesion species concept defines species as evolutionary lineages with the lineage boundaries that define species arising from the forces that create reproductive communities (i.e., cohesion mechanisms)." Key is the realization that both patterns (genealogies) and processes (cohesion mechanisms) are part of the establishment and maintenance of cohesion. The primary focus of the CSC is "genetic exchangeability and/or ecological interchangeability" (Templeton, 2001: 779).

The analytical framework for the cohesion concept has been developed in a series of papers by Templeton and colleagues (Templeton et al., 1987, 1992, 1995; Templeton, 1998a). These methods use a cladogram-based approach to delineate aspects of population processes and genealogical branching. Using the correct and interesting suggestion that information from gene trees often straddles the species boundary, Templeton (1998a) suggested that analysis at such a level can play a major role in understanding both the processes involved and the emergent patterns of divergence. In its most recent manifestations (Templeton, 1998a, 2001), nested clade analysis has been suggested to be of explicit utility in studying the speciation process because it can, in an algorithmic fashion, tease apart the processes and patterns inherent in the speciation process. The method can therefore assess the presence and degree of genetic exchangeability as well as the presence of ecological interchangeability: this allows for empirical examination and rigorous testing of the cohesion species concept.

Templeton's latest (2001) treatments of the CSC explicitly make use of phylogeographic analyses as well as more sophisticated statistical analyses of haplotype networks, neither of which were widely available at the time of the CSC's introduction. We regard the cohesion species concept as possibly the most rigorous framework for exploring microevolutionary histories.

The Genealogical Species Concept

Advocates of the genealogical species concept use a tree-based approach to determine species boundaries but specifically endorse its use outside the framework of the BSC (Baum & Shaw, 1995; Baum, 1992, 1999; Baum & Donoghue, 1995). Echoing Cracraft's definition of the phylogenetic species concept, Shaw (1998: 48) defined a genealogical species as "a basal exclusive group of organisms whose members are all more closely related to each other than they are to organisms outside the group and that contains no exclusive groups within it." In essence, proponents of the GSC argued (e.g., Baum, 1992) that the BSC is confounded by the fact that reproductive isolation is not necessarily an absolute indicator of evolutionary proximity. They articulate the criterion of "exclusivity," identical in its definition to monophyly but asserted to be applicable at any level as the ultimate arbiter of species status (Baum & Shaw, 1995; Baum, 1992; Baum & Donoghue, 1995; de Queiroz & Donoghue, 1988). There is little difference between the GSC and tree-based (phylogeographic) studies within the framework of the BSC, but the proponents of the GSC specifically tailor their definition to incorporate coalescent analyses. We include the GSC in our discussion because its operation explicitly denies the boundary between hierarchic and non-hierarchic systems.

The Phylogenetic Species Concepts

Several versions of the phylogenetic species concept (PSC) have pervaded the literature (see Baum & Donoghue, 1995; de Queiroz, 1998; Goldstein & DeSalle, 2000), contributing to considerable confusion over the term. The PSC has enjoyed at least three definitions, not including those deriving in part from phylogenetic theory yet not explicitly tied either to character state distributions or to monophyly (the evolutionary species concept of Wiley (1978) and the internodal species conception considered to have been held by Hennig (1966; see also Ridley, 1989; Meier & Willmann, 2000)). These definitions include the genealogical species concept (described above) and the monophyletic species concept (Donoghue, 1985), elsewhere referred to as the autapomorphic species concept (Nixon & Wheeler, 1990).

The original PSC explicated by Cracraft (1983, 1989), and elaborated on by Nixon and Wheeler (1990), relies on a character-based approach to delimit species. According to the PSC, a species is defined as "an irreducible (basal) cluster of organisms diagnosably distinct from other such clusters and within which there is a parental pattern of ancestry and descent" (Cracraft, 1989: 35). The term "basal" here refers to "elemental" or "minimal," and is not intended as a reference to relative phylogenetic placement (J. Cracraft, pers. comm.). Character-based diagnosis gives the PSC its operational strength, since all organisms have observable features (characters) and, so the argument goes, can be aggregated into phylogenetic species where appropriate, using either population aggregation analysis (PAA; Davis & Nixon, 1992) or analogous methods (such as cladistic haplotype analysis, or CHA; Brower, 1999). Population aggregation analysis characterizes populations as phylogenetic species if fixed differences are discovered. Although conceived before the upsurge in the use of molecular genetics in conservation, it should be noted that the PSC is agnostic with respect to the kind of character data it incorporates: phylogenetic species may be delineated based on morphological, molecular, behavioral, or other characters with equal rigor. Confusion of the PSC with "morphological" species concepts is therefore spu-

rious. In the example of the buck moth *Hemileuca maia* (Drury) complex (Lepidoptera: Saturniidae), limited genetic data did not provide a diagnosis of host races, but the larval behavior and morphology suffice to diagnose such geographically limited metapopulations as phylogenetic species (Legge et al., 1996).

The operationality of the PSC is a point of contention because (1) operationalism precludes the discovery of entities outside the parameters of the operation itself (Frost & Kluge, 1994; Frost, 2000) and (2) results can be subject to the quality and quantity of data collected (Walsh, 2000). Blanket adherence to a specific sorting methodology is certainly a concern and should be tempered with as much biological evidence as possible before major taxonomic or conservation decisions are made. However, PAA does provide an empirically defensible first cut with respect to such decisions. The sampling issue is of more practical concern: if too few populations or individuals in each population are sampled, overdiagnosis can occur, leading to the delineation of unsubstantiated species; if too few characters are assessed, underdiagnosis can occur, leading valid species to be unrecognized (Davis & Nixon; 1992; Baum, 1992; Mayden & Wood, 1995).

Databases for Analyzing Diagnostics and Constructing Trees

The first step in a rigorous approach to identify putative species or units of protection is the physical construction of a database. Here we first outline some parameters for constructing the databases necessary for species identification, then deal more specifically with the application of the phylogenetic species criterion.

All approaches to diagnosis are susceptible to sampling effects, so the first consideration is to conduct focused taxonomic sampling around the species of interest. Considerable knowledge about the organisms in a study group is necessary to accomplish a reasonable and logical sampling strategy. Sequences can be obtained from many sources including GenBank and colleagues interested in similar questions about particular organisms. Before making comparisons of unknown specimen DNA, the database must be aligned to establish positional similarity (homology) so that any comparisons made with unknown DNA are meaningful. Such alignment can be accomplished using a variety of computer programs such as MALIGN (Wheeler & Gladstein, 1998) or Clustal (Thompson et al., 1994). For indel-free sequences, alignment is generally trivial and can be visualized from within Sequencher (Gene Codes Corporation, 2001). It must be noted here that computationally intensive and sophisticated alignment procedures have been proposed for purposes of phylogenetic reconstruction, and that these may obviate the need for the distinction between primary and secondary homology as generally embraced by systematists (Wheeler, 2000). It remains to be seen whether comparable methods will prove necessary or desirable for lower-level taxonomic or population studies that may not rely on the construction of cladograms and that involve only a few genes. But it is not unlikely that growing computational sophistication will almost certainly be brought to bear on species-level questions to the extent means of optimizing character concordance pertains to analyses addressed at biodiversity stewardship.

An essential but commonly overlooked aspect of generating even a modest database is proper vouchering of specimens and archiving of sequences (Paabo et al., 1992; Whitfield & Cameron, 1994; Ruedas et al., 2000). Each archiving procedure should ensure that diagnostic methods can be reproduced or re-tested if and when the need arises.

Several computer programs allow for the examination of databases using the two broadly articulated phylogenetic approaches. The population aggregation approach is most readily accomplished in programs such as MacClade (Maddison & Maddison, 2000), WinClada (Nixon, 1999), TNT (Goloboff et al., 2004), or PAUP* (Swofford, 2001). Figure 1 demonstrates the utility of the PAA approach in determining species status in muntjac (*Muntiacus* Rafinesque). In this study, Amato et al. (1999) used mitochondrial DNA sequences from extant and museum specimens to construct hypotheses about species status in this group of cervids (Cervidae: Muntiacinae). Through comparison of 16s mitochondrial ribosomal DNA (16s mt rDNA) sequences from the 70-year-old type specimen of *M. rooseveltorum* (Osgood, 1932) with recently collected material, this methodology helped enable the re-discovery of *M. rooseveltorum* (Amato et al., 1999). In Figure 1, note that the diagnostic nucleotide site specific to an aggregated group of muntjac tentatively identified as *M. rooseveltorum* is also present in the type specimen (noted as *M. rooseveltorum* Type; nucleotide position 276 is a G in the putative and type *M. rooseveltorum* vs. an A in all other muntjac), indicating aggregation of the type *M. rooseveltorum* specimen with the putative *M. rooseveltorum.* In this case, those putative *M. rooseveltorum* can be synonymized with the type and the nomenclature of the group simplified (Amato et al., 1999). Also

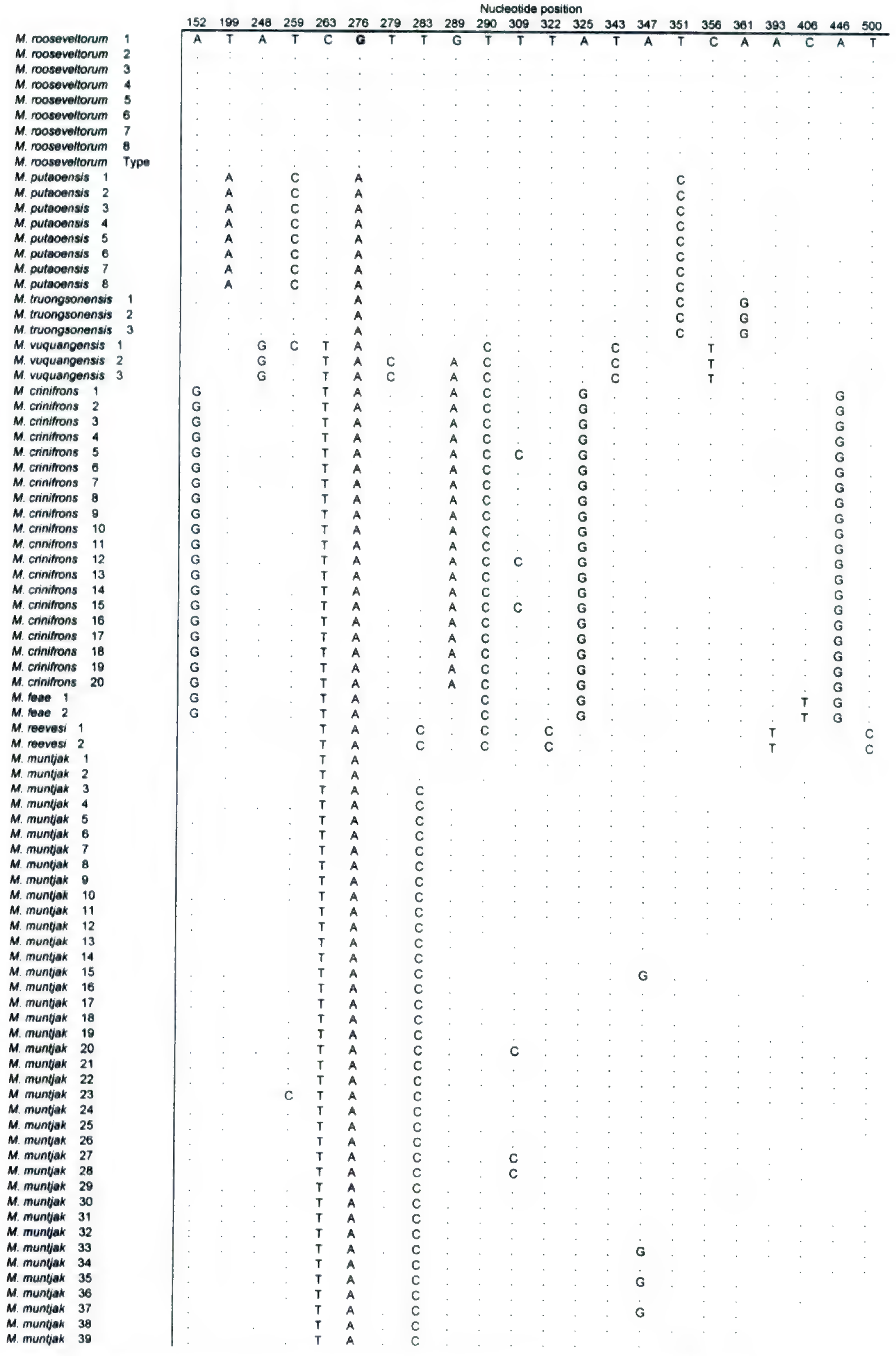

Figure 1. An example of PAA from the muntjac species study (Amato et al., 1999). The figure shows variable nucleotide positions including several diagnostic sites in the 16s mt rDNA of multiple individuals of muntjac species. Position 1 in the region sequenced corresponds to position 2305 in the *Bos taurus* mitochondrial DNA, complete genome (GenBank Accession Number: AB074962). The word Type after the binomial indicates the sequence obtained from the type specimen of *M. rooseveltorum* to which recently collected putative *M. rooseveltorum* specimens were compared. Shaded area indicates nucleotide position diagnostic for *M. rooseveltorum*. Dots (.) indicate sequence identity to the reference sequence on the first line. Colons (:) indicate missing data.

shown in Figure 1 are additional variable nucleotide positions for this study group to demonstrate the methodology. For example, nucleotide position 259 would not be considered diagnostic for species *M. putaoensis* because although all members of the species sampled share a C at that position, so do individuals of other species. Positions 279, 283, 289, and 347 in Figure 1 do not provide information for species identification because they are either variable within or shared between species. The nature of these sites and the lack of diagnosability highlights the necessity for broad taxonomic sampling to avoid the problem of overdiagnosis.

Generating trees is most commonly undertaken using TNT (Goloboff et al., 2004), PAUP* 4.01b (Swofford, 2001), NONA (Goloboff, 1997), MEGA (Kumar et al., 1994), or PHYLIP (Felsenstein, 1998). In using tree-based diagnostics to delineate groups of organisms, a data file with an undetermined individual is placed into the correct format for the program to be used and a phylogenetic analysis algorithm is chosen to generate a hypothesis of relationships. Certain approaches are more amenable to diagnosis using this approach than others. We prefer the parsimony approach in our work because it results in hypotheses where characters are explicitly tied to groups of individuals and may therefore be regarded as diagnostic where appropriate. A variety of other techniques have also been used as algorithms to generate tree-based hypotheses of species identification.

A potentially confounding element to character-based diagnostics is the possibility of overlapping or conflicting aggregations. Clearly the presence of only one or a few putatively diagnostic base pair characters is suspicions, and we can only reiterate that a concordance of character data is desirable before any decision-making process surrounding a conservation issue is completed.

Tree- and Character-Based Approaches to Species Delineation

Sites and Crandall (1997) have suggested wisely that a logically defensible technique for identifying species enhances the scientific as well as legislative defensibility of species-based conservation initiatives. It is imperative that the logical basis of philosophically disparate techniques and analytical approaches be evaluated as a prelude to their use in conservation programs. Despite its generalizability, the PSC remains controversial for a number of reasons, the most trivial of which stem from confusion of unrelated phylogenetic species concepts (e.g., Meffe & Carroll, 1997; Shapiro, 2002) or the perpetuation of non-scientific arguments. More significant is the distinction between character-based and tree-based diagnoses. Although these have been held at cross purposes, the central issue is not necessarily which to prefer exclusively, but rather which to proceed with first in delineating species, whether by molecular, morphological, or behavioral data. The distinction between tree- and character-based delineation schemes may seem artificial, as trees are, after all, based on characters. As will be seen, such is not always the case in practice, or in the arguments leveled against character-based approaches.

Many discussions have centered on the notion of theory neutrality in species concepts versus the incorporation of theory surrounding biological processes. It has been argued (e.g., Goldstein & DeSalle, 2000) that the theory neutrality of character-based phylogenetic species concepts is a desirable attribute, as is its focus on the occurrence of fixed character state differences. These ideas have met with mixed responses, and some authors have even advanced the notion that the PSC is somehow at odds with evolutionary theory, a characterization we find misplaced. Specifically, the term "pattern"—an allusion to the political calumny of pattern cladistics or pattern cladism dating to the 1980s—is leveled with increasing frequency at authors adopting a character-based view. Baum and Donoghue (1995) contrasted their genealogical species concept, which they termed as "history based" with the PSC, implying the latter was a non-evolutionary outgrowth of the oft-reviled and, in our view, mythical school of pattern cladistics. They used a hypothetical scenario in which species with two quite distinct flower morphologies appear as sisters to the exclusion of individuals superficially identical to one of the forms. Notwithstanding the fact that a rigorously analyzed data matrix would have to include enough other characters to overwhelm the flower morphology gestalt in order for such a hypothesis of relationship to obtain, their example fails because it contains at most two taxa, and when collapsed to a two-terminal statement, it is information-free. A more pointed example would involve three or more putative species with individuals from each, concatenated across a tree. As it stands, Baum and Donoghue's hypothetical example really illustrates the potential pitfalls of forcing reticulate data into a hierarchy-generating framework. Simply stated, phylogenetic trees are hollow beyond the characters on which they are based.

It has also been pointed out, and rightly so, that no concept is truly theory-neutral (Templeton,

2001). However, it seems obvious that the more theory-laden a given conception of what a formal species is, the less generalizable it becomes, and hence the more difficult to test species boundaries in the first place. This may be an example of biologists disagreeing over where along the evolutionary trajectory of speciation to focus recognition and conservation efforts. The phylogenetic species criterion is in fact quite consistent with the body of microevolutionary theory: no proponent of the PSC would deny that the underlying rationale for preferring fixed character states as diagnostic is underlain by the inference of interbreeding (Goldstein & Brower, 2002). In other words, theory neutrality is not equivalent to theory incompatibility. In our view, the protracted semantic debate about theory neutrality per se is a distraction.

The most incisive discussions have focused on the kinds of data relevant to species delineation, the methods for analyzing them, the interpretation of results, and the implications of tree- versus character-based methods. Following Davis and Nixon (1992), most authors admit a boundary demarcating phylogeny (nested hierarchies of species relationships) from tokogeny (reticulating networks of interbreeding individuals): below this boundary, the hierarchic output of cladistic analysis is inaccurate, and Davis and Nixon's method is designed primarily to identify aggregates of individuals (phylogenetic species) suitable as terminals in phylogenetic analysis. Disagreement appears over whether the methods and interpretive schemes of population genetics and systematics should be similarly restricted on one or the other side of this hypothetical line, or more wantonly amalgamated in the delineation of species or conservation units (Goldstein & Brower, 2002).

The Relationship between Diagnosability and Reciprocal Monophyly

Phylogenetic analyses, regardless of their operational framework, have been criticized as exclusive arbiters of species status on the grounds that it is illogical to represent reticulate sets of relationships as hierarchical (Davis & Nixon, 1992; Vogler & DeSalle, 1994; Luckow, 1995; Goldstein et al., 2000; Goldstein & DeSalle, 2000), or more pointedly, to elucidate relationships among things without first defining their boundaries is backwards (Mallet, 1995). Since individuals in reticulating populations are not legitimately represented as related hierarchically, finding hierarchy below the species level may simply be an artifact of the analysis (Goldstein & DeSalle, 2000), particularly when distance-based methods are used (cf. Ferguson, 2002).

Rosenbaum et al. (2000) have analyzed the genetics of the species boundary of populations of right whales, *Eubalaena* spp. (Balaenidae). Prior to their analysis two nomenclatural units were recognized, the North Atlantic Right Whale *Eubalaena glacialis* Müller in the Northern Hemisphere and the Southern Right Whale *Eubalaena australis* Desmoulins in the Southern. Despite a paucity of morphological information (summarized in Rosenbaum et al., 2000) supporting the nomenclatural status of these units, they were able to justify, using mitochondrial d-Loop sequences, the resurrection of the North Pacific Right Whale *Eubalaena japonica* Lacépede as the third of three diagnosably distinct populations of right whales. Population aggregation analysis revealed at least three fixed nucleotide sites in each of the three distinct units in their study. The same three entities appear as well-supported in a cladistic analysis (Fig. 2). The resultant tree shows that the Northern Pacific and Southern Hemisphere whales are sister groups with the Northern Atlantic whales immediately outside. The topology suggests, however, that the Northern Pacific whales do not comprise a sister group to their nomenclatural conspecifics. While this result is interesting, it is not relevant to the designation of the three populations—North Atlantic, North Pacific, and Southern Hemisphere—as three independent diagnosable units.

In the study by Rosenbaum et al. (2000), reciprocal monophyly and diagnosis coincide, but such agreement is not the only possible scenario that obtains when diagnosis and tree building methods are used on the same data. Character fixation and the appearance of reciprocal monophyly in a phylogenetic analysis need not coincide, a seemingly trivial observation explicated by Goldstein and DeSalle (2000). Of significance is whether the results of population aggregation analysis or phylogeographic analysis should be taken at face value when they disagree. Brower (1999) illustrated some theoretical examples where two entities are found to be reciprocally monophyletic, and yet no diagnostics exist for the two entities being scrutinized. Such an outcome is particularly likely when distance methods such as neighbor-joining are employed (Goldstein & DeSalle, 2000).

Conversely, diagnosis can sometimes be demonstrated for entities where a tree-based analysis shows no reciprocal monophyly (Vogler & DeSalle, 1994; Goldstein & DeSalle, 2000). This is not uncommon in cases involving short divergence times or populations of wildly asymmetrical sizes that en-

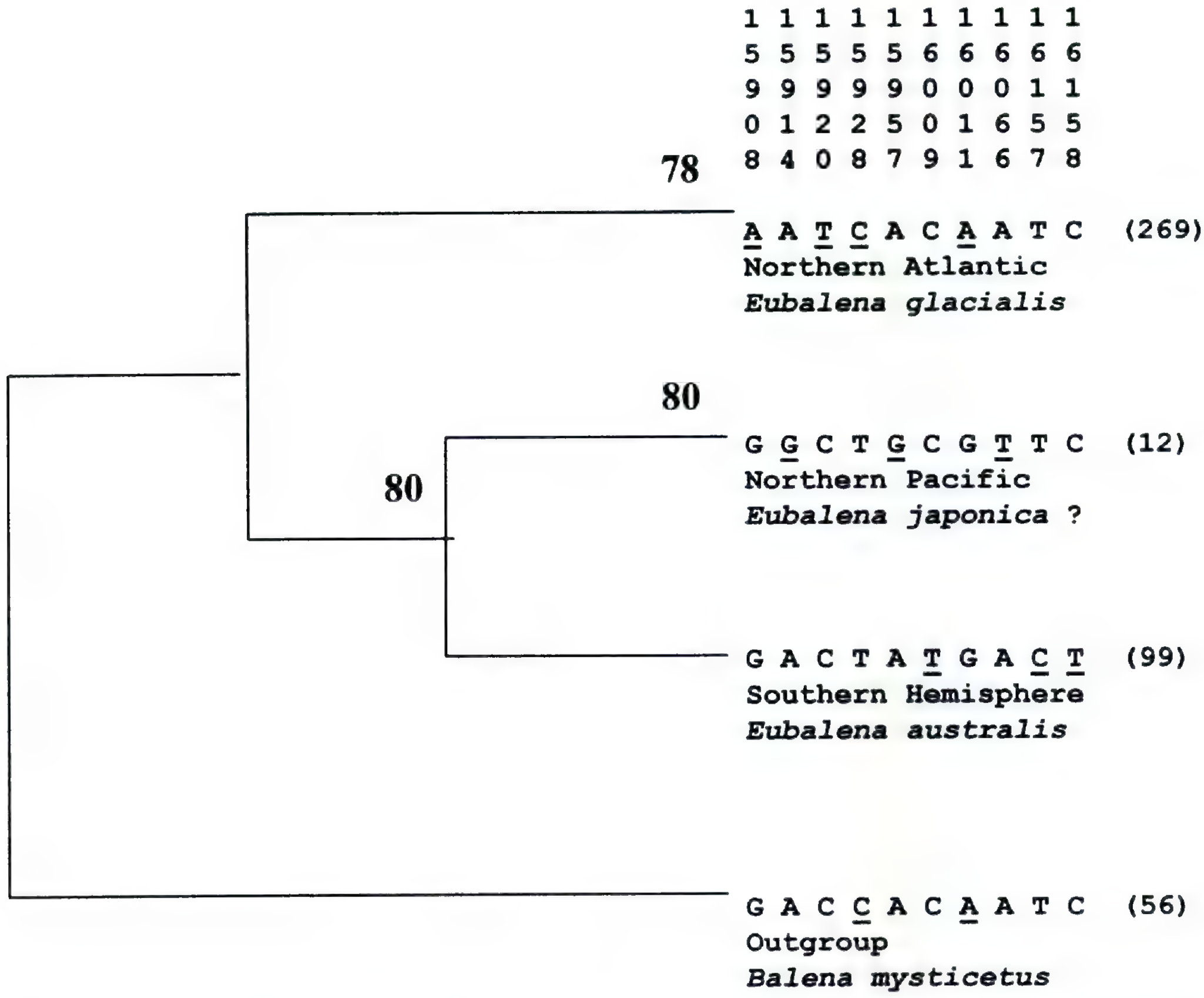

Figure 2. Reciprocal monophyly and diagnosis coincidence in right whales. Figure redrawn from Rosenbaum et al. (2000). Numbers to the right of the tree indicate position in the mitochodrial d-Loop where the nucleotide information comes from. Character state for that position is listed for each of the three major geographic populations of *Eubalaena*. Underlined bases indicate positions and state (G, A, T, or C) that is diagnostic for that population. Numbers on nodes indicate jackknife support values for that node as given in Rosenbaum et al. (2000).

able differential fixation events. Theory predicts that reciprocal character fixation is likely to occur more quickly than true reciprocal monophyly (and certainly before reproductive isolation; cf. Harrison, 1998), and to the extent it is recognized that such cases involve recently diverged entities, there is no reason to dismiss independent management agendas on account of intranominal paraphyly.

Character Extinction and "Speciation by Remote Control"

Perhaps the most controversial ramification of the PSC is the idea that observably distinct lineages arise by virtue of the extinction of polymorphic intermediates. Templeton (2001: 789) has referred to this "ludicrous" implication as "speciation by remote control." The idea is, of course, antithetical to any conception that requires speciation to be accompanied by adaptation or reproductive isolation. However, the recognizability of different species relies fundamentally on the fixation of alternative character states in different populations; it is readily seen that the extinction of polymorphic intermediates is a necessary step in what we might refer to as "phylogenetic speciation" (Nixon & Wheeler, 1992; Vogler, 1994). This in no way precludes the recognition of more distantly diverged, genetically cohesive lineages, or their descriptions as species. Indeed, we would reject the idea of appending formal taxonomic epithets on the basis of a single mitochondrial nucleotide polymorphism, for example. The PSC is not explicitly tied to processes by which groups of organisms attain stability; the PSC is concerned, rather, with maximizing our ability to understand and reconstruct macroevolutionary history at the finest possible resolution regardless of what may or may not be predicted to occur in the future, which is outside the purview of science (Wyner et al., 1999).

Vogler and DeSalle (1993, 1994) established a diagnostic system for identifying boundaries of putative conservation or management units in the

Northeastern Beach Tiger Beetle, *Cicindela dorsalis dorsalis* Say (Coleoptera: Carabidae). This federally threatened insect has a disjunct distribution along the Northeast Atlantic Coast, where it appears on the beaches of Martha's Vineyard and the Chesapeake Bay, but has been extirpated from intermediate locations in Rhode Island, Connecticut, New York, and New Jersey (fig. 1, Goldstein & DeSalle, 2003: 1995). Of the four valid subspecies of *C. dorsalis*, none appears as diagnosable or as monophyletic, reciprocally or otherwise, in the analysis by Vogler and DeSalle (1993). The diagnostic system differentiating the Martha's Vineyard population from the Chesapeake Bay populations is based on the detection of a fixed nucleotide position in the mitochondrial DNA of these, and is corroborated by larval behavioral differences, hypothesized adaptation to northern, ocean-fronted beaches versus more southerly bay-fronted beaches visited by different disturbance regimes (Nothnagle & Simmons, 1990). In this case, the ongoing reintroduction strategy of maintaining the integrity of the New England metapopulation, based in large part on that last ecological observation, is corroborated by the genetic data.

More recently, however, Goldstein and DeSalle (2003) examined the genetics of the extirpated historical populations on the Northeast United States coast between Martha's Vineyard and the Chesapeake Bay and found that the haplotype framework demarcating these population aggregates is eroded when the historical haplotypes gathered from museum specimens are considered (fig. 1, Goldstein & DeSalle, 2003, available from the authors). Historical populations from Rhode Island and New York are polymorphic for the diagnostics and as such comprise genetic "linker populations" (Vogler, 1994) between Martha's Vineyard and the Chesapeake Bay. Our then-unpublished interpretation of these data was characterized in Avise's (2001: 1828) review of an unrelated edited volume (Wheeler & Meier's (2000) Species Concepts and Phylogenetic Theory, which did not feature any of our work), as having "caught a speciation event in the act." In point of fact, we have been careful to characterize this system, both in lecture forums and our recent publication (Goldstein & DeSalle, 2003), as agnostic with respect to nomenclature and the evolution of reproductive isolation and more importantly as a *reductio ad absurdum* that serves merely to illustrate the relationships among extinction, fixation, and diagnosability.

In that context, the example of *Cicindelea dorsalis* illustrates a solution to the pseudo-paradox known as Woodger's dilemma (Nixon & Wheeler, 1992; Goldstein & Brower, 2002), which asks how more than one species can possibly exist when parents and offspring are necessarily conspecifics. As species differentiate, events must arise where a parent and its offspring belong to different recognized species, a troubling concept for many biologists, especially those who conflate reproductive continuity of life with hierarchic continuity in the form of phylograms. In contrast, the PSC in effect emphasizes discontinuity as the initial means by which different species become recognizable as such. The extinction of polymorphism (as with the extinction of the *C. dorsalis* linker populations) enables the recognition of multiple entities. We believe it naïve to deny the role of extinction in macroevolution, and hence find no fault with so-called speciation by remote control so long as it is recognized merely as an early stage in potentially more adaptive evolutionary divergence, and one that potentially enables the elucidation of macroevolutionary history by identifying suitable terminals in phylogenetic analysis.

Conclusion

By using character state distributions to recognize phylogenetic species, systematists have argued that species form the elemental currency of biodiversity (but see Bachmann, 1998), and as such have pushed the species level below traditional limits recognized by the biological species concept. Proponents of the BSC and paradigms rooted in population genetics have argued simultaneously that character-based diagnoses enable the recognition of too many entities (Avise, 2000), but that tree-building algorithms are legitimately used at any level. Although evolutionary processes that comprise the focus of many well-articulated conservation genetic paradigms (Moritz, 2002) are an appropriate target of conservation efforts in the abstract, we maintain that the goals of conservationists are most successfully realized by stewarding the ecological context that enables natural selection to proceed, i.e., by protecting expansive areas supporting large populations where the impacts of genetic drift are minimized. An understanding of patterns of character distributions is in no way inconsistent with these goals and is likely to help pinpoint populations and areas in need of critical protection.

As has been observed repeatedly, methods of population genetics are now routinely used in systematics, while cladistic hypotheses appear regularly in intraspecific (or intra-nominal) cladograms. Moritz (2002: 243) referred to Goldstein et al.

(2000) as making the "misplaced assertion" that "the description of biological diversity should be solely within the realm of systematics and exclusive of population genetic and evolutionary theory." This is a considerable exaggeration of our statement (Goldstein et al., 2000: 127) to the effect that "the conclusions of systematics and population genetics complement each other best—and are most successfully realized—when it is recognized that the methods of each field are designed to address different kinds of questions and are applied appropriately as such" and that confounding disparate logical frameworks or "simply combining desirable aspects of each field into a philosophical patchwork does not engender a more powerful form of inquiry." Our point is simply that systematic progress should proceed unhindered by microevolutionary assertions.

Neglecting the presence or absence of diagnostic characters when interpreting the limits of hierarchic inference has resulted in several related classes of data misinterpretation (Goldstein et al., 2000: 123), including the interpretation of frequency or phenetic data as relevant to species diagnosis, the interpretation of raw character data as adaptive, and the interpretation of reticulate systems as nested hierarchies (Goldstein & DeSalle, 2000: 127). The uncritical acceptance of reciprocal monophyly as an exclusive criterion for species recognition or delimitation of ESUs is not sufficient to address the aims of biological description or conservation. We have argued that the criterion of reciprocal monophyly, while often consistent with character-based approaches to species diagnosis, must be interpreted cautiously below the level where reticulate patterns overwhelm hierarchical ones, the theoretical boundary defined by the phylogenetic species criterion (Nixon & Wheeler, 1990), and most especially when distance-based methods are used to generate trees.

Species represent the nexus of systematics and population genetics, and the need for recognition of species and conservation units grows with the ongoing biodiversity crisis. Although debates over species concepts and conservation persist, most participants in these debates recognize the occurrence of qualitatively different kinds of organismal groups. It is our thesis that disagreements have arisen primarily as a result of confusion over where along the spectrum of species ontogeny (Harrison, 1998) the operations of diagnosability, formal taxonomy, and coalescence properly lie, and we argue that these disagreements are particularly frequent when species concepts compete at the shallowest of evolutionary divergences where the so-called species boundary is most tricky. Whereas some solutions to the species problem strive to generalize species concepts such that they can incorporate as many of these as possible (de Queiroz, 1998), while others explicitly incorporate microevolutionary mechanisms to account for the means by which cohesive species arise (Templeton, 1989), the phylogenetic species criterion simply provides a generalizable framework for recognizing minimal observable groups that might be suitable as terminals in (hierarchical) phylogenetic analysis.

We suggest that a logical starting point for studies of species origin or species boundaries based on organismal attributes can be found in population aggregation analysis (PAA; Davis & Nixon, 1992) or modifications thereof (e.g., cladistic haplotype aggregation; Brower, 1999). This is not to say that more in-depth analyses exploring reciprocal monophyly or other such phenomena are categorically ill-placed; the incorporation of diagnostic characters in the circumscription of species or conservation units does not necessitate the impractical notion that single character systems be accepted as de facto proof of species or conservation status. However, the circumscription of any status in the absence of diagnosis is both scientifically suspect and actually dangerous when employed in the context of wildlife protection: if individual organisms cannot be recognized as members of a species, their protection cannot be addressed practically or realistically.

The phylogenetic species criterion—that the first and foremost condition of telling species apart is on the basis of diagnostic characters—is a necessary condition of species delineation. We maintain that diagnostic character states in the form of fixed genetic differences are necessary, but not always sufficient, to delineate species and conservation units. Behavioral and ecological requirements are often at least as important as molecular data. In contrast to the case of the buck moth *Hemileuca maia* complex, where a lack of discernable diagnostic differences was overwhelmed by the ecological and host plant associations of geographically distinct races (Legge et al., 1996), the case of the Northeastern Beach tiger beetle involves the trivial fixation of a single base pair that is actually accompanied by significant behavioral and ecological differences between metapopulations. In neither case do the putative units of conservation management appear as monophyletic or reciprocally monophyletic. Elucidation of reciprocal monophyly may thus represent a legitimate heuristic that strengthens the conclusions of character-based diagnostics provided the methods used in tree-building are consistent

with the elucidation of those diagnostics and provided that the trees are not themselves interpreted as phylogenies per se.

The distinction between character- and tree-based approaches to species delineation is not a simple dichotomy, nor is it useful to set the notions of character state distribution pattern at odds with evolutionary process. Clearly articulated species concepts and operational applications are critical to realizing the potential of genetics in conservation biology contexts. As such, species concepts and their articulation are extremely important to a logical and clear use of systematic and population genetic analyses in conservation. Avise et al. (1987: 490) have suggested that "too many systematists and population geneticists continue to operate in largely separate realms, employing different languages and concepts to address issues that should be of importance to all." The major two endeavors of evolutionary biology—systematics and population genetics—do indeed complement one another, and there is no applied subdiscipline in all of biology that can benefit more from that complementarity than conservation biology. We point out, however, that producing chimeric philosophical frameworks (such as imposing tree-building methods onto reticulate systems) does not enhance that complementarity. If phylogenetics were stripped of the recognition of species boundaries, our ability to articulate the context from within which biological uniqueness and importance becomes apparent would be irrevocably lost. The concept of the species boundary, more precisely the discontinuity in character state distributions as recognition criteria, is critical not just practically as a means around which to design an effective information retrieval system for describing and studying biodiversity, but as a theoretical guidepost for exploring both micro- and macroevolution. To endorse a concept that fails to address these twin goals simultaneously is to hamstring the endeavors of scientific progress and biological conservation.

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ADAPTIVE RADIATION AND REGULATORY GENE EVOLUTION IN THE HAWAIIAN SILVERSWORD ALLIANCE (ASTERACEAE)[1]

Michael D. Purugganan[2] *and Robert H. Robichaux*[3]

ABSTRACT

The Hawaiian silversword alliance is a premier example of adaptive radiation, and serves as a model for exploring the genetic basis of morphological diversification in plants. Molecular analyses at macroevolutionary and microevolutionary scales suggest that rapid and extensive diversification in reproductive and vegetative form in the silversword alliance may be linked to alterations in the tempo and mode of regulatory gene evolution. Unfortunately, the silversword alliance also epitomizes the conservation challenges confronting the biotas of oceanic archipelagos, especially the threats posed by alien species. Taking action now to prevent extinction is key to further exploring adaptive radiation and its link to genome evolution.

Key words: adaptive radiation, *APETALA1*, *APETALA3*, extinction, *GAI*, Hawaiian silversword alliance, regulatory gene evolution.

ADAPTIVE RADIATION, WILSON'S CONJECTURE, AND THE GENETIC BASIS OF MORPHOLOGICAL DIVERSIFICATION

Adaptive radiation is a key process in the evolution of life's diversity (Carlquist, 1974; Givnish & Sytsma, 1997; Schluter, 2000). Lineages undergoing adaptive radiation are especially prominent in the biotas of oceanic archipelagos and continental rift lakes, where conditions appear to favor unusually high rates of evolutionary innovation. Well-known examples include the Galapagos finches (Lack, 1947; Grant, 1986), Hawaiian honeycreepers (Tarr & Fleischer, 1995), Hawaiian drosophilids (Carson & Kaneshiro, 1976; Kaneshiro et al., 1995), Hawaiian silversword alliance (Carr, 1985; Robichaux et al., 1990), and African rift lake cichlids (Meyer et al., 1990). Such lineages offer a special opportunity for exploring the genetic basis of morphological diversification. The recency and extensiveness of the diversification enhance the prospects for detecting the underlying molecular genetic signatures, thereby allowing for direct comparison of the tempo and mode of morphological and molecular evolution.

Paradoxically, rates of morphological evolution are generally not correlated with rates of molecular evolution (Wilson et al., 1974; King & Wilson, 1975), an early observation reinforced by more recent studies on the evolution of structural genes in lineages exhibiting adaptive radiation. The cytochrome b and mitochondrial control regions of African rift lake cichlids, for example, do not exhibit any significant degree of interspecific molecular divergence despite the spectacular diversity in morphology (and coloration) among the species (Meyer et al., 1990). Such limited differentiation in structural genes is also evident in other lineages exhibiting adaptive radiation (Witter & Carr, 1988; Hodges & Arnold, 1994) and suggests that structural gene evolution may not be the key to rapid and extensive diversification in organismal form.

This apparent paradox led Allan Wilson and others to propose that morphological diversity among species arises primarily from regulatory gene evolution within developmental systems rather than from structural gene evolution (Wilson et al., 1974; King & Wilson, 1975; Wilson, 1976). This conjecture is supported indirectly by comparative developmental work in a number of taxa, which reveals that diversity in form among species arises by transformation of ontogenetic trajectories (Patel, 1994; Carroll, 1995; Warren et al., 1995; Lowe & Wray, 1997). These changes in trajectories result in

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[2] Department of Genetics, Box 7614, North Carolina State University, Raleigh, North Carolina 27695, U.S.A. michael_purugganan@ncsu.edu.

[3] Department of Ecology and Evolutionary Biology, University of Arizona, Tucson, Arizona 85721, U.S.A. robichau@u.arizona.edu.

evolutionary innovations in morphology.

Regulatory genes represent a class of loci that control the expression of other genes (Doebley, 1993; Purugganan, 1998). These genes play central roles in the genetic architecture of eukaryotic development, since they guide ontogenetic trajectories and thus specify organismal morphology (Meyerowitz, 1997). Developmental genetic studies in plants have demonstrated that classes of regulatory genes control the differentiation of various reproductive and vegetative structures (Meyerowitz, 1997; McSteen & Hake, 1998). Thus, there has been increasing interest in understanding the evolution of regulatory genes, many of which have been shown to encode sequence-specific, DNA-binding transcriptional activators (Doebley, 1993; Purugganan, 1998). Indeed, if Wilson's conjecture is correct, an assessment of the forces shaping regulatory gene evolution may prove critical to understanding adaptive radiation.

Studies of regulatory gene evolution have focused primarily on macroevolutionary patterns of gene diversification (Purugganan, 1998; Cronk, 2001). Recent phylogenetic analyses of several regulatory gene families reveal that most developmental systems evolve by duplication and divergence of paralogous loci (Sidow, 1992; Atchley et al., 1994; Ruddle et al., 1994; Purugganan et al., 1995; Theissen et al., 1996; Bharathan et al., 1997; Purugganan, 1997). Moreover, regulatory genes appear to evolve faster than typical structural loci (Purugganan & Wessler, 1994; Purugganan, 1998; Ting et al., 1998), and these elevated molecular evolutionary rates may be associated with developmental alterations and morphological diversification. Variation in the expression of regulatory genes has also been observed among divergent lineages. Orthologues of genes that control embryonic development in *Drosophila melanogaster* Meigen, for example, have been examined in a number of insect and crustacean taxa (Patel, 1994; Carroll, 1995; Warren et al., 1995). The studies reveal expression pattern diversity that is correlated with intertaxon variation in developmental patterns and morphological features.

Patterns of regulatory gene evolution evident at the macroevolutionary scale must have their origins in molecular variation that occurs within and among populations. Investigating patterns of variation at the population level, where evolutionary forces play themselves out to determine the fates of alternate alleles (Doebley, 1993; Palopoli & Patel, 1996; Purugganan, 1998, 2000), is thus key to understanding the evolutionary dynamics of these developmental control genes. A molecular population genetic approach provides a framework for assessing how selection and other factors affect variation at regulatory loci, and for delineating mechanisms that lead to evolutionary diversification (Purugganan, 2000).

Recent work in *Arabidopsis thaliana* (L.) Heynh., *Zea mays* L., and *Drosophila melanogaster* suggests that regulatory genes can harbor significant levels of molecular variation (Gibson & Hogness, 1996; Hanson et al., 1996; Richter et al., 1997; Ting et al., 1998; Wang et al., 1999; Olsen et al., 2002), and that selective (Doebley et al., 1997; Purugganan & Suddith, 1998), demographic (Purugganan & Suddith, 1999), and recombinational (Doebley et al., 1997) forces interact to pattern variation at these loci. Analysis of the *Arabidopsis* Heynh. floral developmental pathway reveals contrasting patterns of selection in the coding regions of floral regulatory loci (Olsen et al., 2002). Moreover, there appears to be evidence for selection in the promoter region of at least one gene, the inflorescence architecture gene *TFL1* (Olsen et al., 2002). Analysis of the *tba1* locus in *Zea* L. also highlights the role of selection in shaping promoter variation at a regulatory gene during the evolution of domesticated maize (Wang et al., 1999). In addition, molecular variation at this locus, as well as at *Arabidopsis CAL* (Purugganan & Suddith, 1998) and *Drosophila* Fallén *Scabrous* (Lai et al., 1994), *Delta* (Long et al., 1998), and *Ultrabithorax* (Gibson & Hogness, 1996) loci, is associated with functional variation in regulatory gene activity. These and related studies have begun to shed light on the evolutionary forces that determine the extent and patterning of regulatory gene variation and the phenotypic consequences of diversification at the molecular level.

Morphological Diversification and Regulatory Gene Evolution in the Hawaiian Silversword Alliance

The Hawaiian silversword alliance is a premier example of adaptive radiation (Carr, 1985; Robichaux et al., 1990). The silversword alliance includes 30 species in three endemic genera: *Argyroxiphium* DC., *Dubautia* Gaudich., and *Wilkesia* A. Gray. The species grow in habitats as varied as exposed lava, dry scrub, dry woodland, mesic forest, wet forest, and bog, and range in elevation from less than 100 m to more than 3700 m. In addition to their great ecological diversity, the species exhibit exceptional morphological diversity, extending to most aspects of reproductive and vegetative form.

With respect to reproductive traits (Carr, 1985), the species differ greatly in head (or capitulum) and

flowering stalk (or capitulescence) architectures. All *Wilkesia* and *Dubautia* species have discoid heads, whereas all *Argyroxiphium* species have radiate heads. Head sizes vary from as few as 2 flowers per head (e.g., in *D. pauciflorula* H. St. John & G. D. Carr) to as many as 650 flowers per head (e.g., in *A. sandwicense* DC. subsp. *macrocephalum* (A. Gray) Meyrat). Flowering stalks vary in shape and number of heads, ranging from as few as 3 heads per flowering stalk (e.g., in *D. ciliolata* (DC.) D. D. Keck subsp. *glutinosa* G. D. Carr) to as many as 600 heads per flowering stalk (e.g., in *A. sandwicense* subsp. *macrocephalum*). The large flowering stalks of *Argyroxiphium* and *Wilkesia* species tend to dominate plants in flower. Floral organs also exhibit qualitative and quantitative differences among the species, including variation in corolla, pappus, and ovary sizes and style morphologies. In addition, the species differ in reproductive mode, with most being polycarpic, but some (e.g., *A. sandwicense* subsp. *macrocephalum* and *W. gymnoxiphium* A. Gray) being predominantly monocarpic.

With respect to vegetative traits (Carr, 1985; Carr et al., 1989; Robichaux et al., 1990), the species exhibit a wide range of growth forms. All *Argyroxiphium* and *Wilkesia* species are rosette shrubs, with the rosettes being sessile in some species (e.g., *A. caliginis* C. N. Forbes) and elevated on woody stems in others (e.g., *W. gymnoxiphium*). Most *Dubautia* species are shrubs, though they range from large, erect forms (e.g., *D. waianapanapaensis* G. D. Carr) to small, spreading forms (e.g., *D. scabra* (DC.) D. D. Keck subsp. *scabra*) and cushion forms (e.g., *D. waialealae* Rock). One *Dubautia* species is a liana (*D. latifolia* (A. Gray) D. D. Keck), and three can grow as small trees (*D. arborea* (A. Gray) D. D. Keck, *D. knudsenii* Hillebr. subsp. *knudsenii*, and *D. reticulata* (Sherff) D. D. Keck). The species also differ greatly in leaf shape, structure, and size. For example, leaves range from as small as 5 mm in length (e.g., in *D. ciliolata* subsp. *ciliolata*) to as large as 500 mm in length (e.g., in *W. gymnoxiphium*).

Molecular phylogenetic analyses provide compelling evidence that the silversword alliance is monophyletic, having descended from species in the "Madia" lineage of North American tarweeds (Baldwin et al., 1991; Baldwin & Robichaux, 1995; Baldwin, 1996, 2003). Cytogenetic data indicate that the Hawaiian species are tetraploids, in contrast to the basally diploid condition in the most closely related species within the "Madia" lineage (Carr & Kyhos, 1981, 1986; Baldwin, 1996; Carr, 2003). Recent analyses of floral homeotic gene duplications further indicate that the Hawaiian species are allotetraploids, deriving from an ancient interspecific hybridization event involving species in the two lineages containing the modern *Anisocarpus scabridus* (Eastw.) B. G. Baldwin and *Carlquistia muirii* (A. Gray) B. G. Baldwin, respectively (Barrier et al., 1999, 2001). Compared to species in the silversword alliance, the North American tarweed species exhibit substantially less morphological and ecological diversity.

The extensive diversification of the silversword alliance appears to have occurred rapidly (Baldwin, 2003). Based on a calibrated rate-constant ITS phylogeny (or "chronogram"), Baldwin and Sanderson (1998) estimated a maximum age for the most recent common ancestor of the silversword alliance of 5.2 ± 0.8 million years, which closely approximates the age of Kauai, the oldest current high island in the archipelago. Using lineage-branching times based on the calibrated ITS phylogeny, Baldwin and Sanderson (1998) further estimated a minimum rate of diversification of 0.56 ± 0.17 species per million years, which is high compared to continental lineages undergoing diversification (Baldwin, 2003).

EVOLUTION OF GENES REGULATING REPRODUCTIVE DEVELOPMENT

The molecular genetics of plant reproductive development has been the subject of intense study in recent years (Yanofsky, 1995; Liljegren & Yanofsky, 1996), such that more is likely known about the genetics of floral development than that of any other plant developmental system. Much of this work has been carried out in *Arabidopsis thaliana*, where several genes that regulate floral development have been identified. These regulatory loci have been referred to as floral homeotic genes, with mutational lesions in the genes resulting in the formation of aberrant organ types in flowers. These loci include floral meristem identity genes such as *APETALA1* (*AP1*) (Gustafson-Brown et al., 1994; Mandel et al., 1992; Bowman et al., 1993; Irish, 1998), and floral organ identity genes such as *APETALA3* (*AP3*) (Bowman et al., 1991; Jack et al., 1992; Irish & Yamamoto, 1995).

The *Arabidopsis AP1* gene controls the specification of floral meristem identity as well as sepal and petal organogenesis (Bowman et al., 1993; Irish, 1998). Mutants at this locus display loss of sepals and petals and conversion of floral meristems into partial inflorescence-like shoots (Bowman et al., 1993; Irish, 1998). The *Arabidopsis AP3* gene is a floral organ identity gene that regulates petal and stamen development; mutants at this lo-

cus display homeotic transformation of these organs to sepaloid and carpelloid structures (Bowman et al., 1991). Quantitative trait locus (QTL) mapping studies further show that changes in petal and stamen sizes in *Arabidopsis* map to a region that includes *AP3* (Juenger et al., 2000). The function of the related *AP3*-like *Lycopersicon* Miller *TM6* paralogue is unknown, although its expression pattern is consistent with roles in petal and stamen development (Pnueli et al., 1991; Kramer et al., 1998). Orthologues in the Asteraceae to both *AP1* and *AP3* have been isolated in *Gerbera* L., and these loci appear to have functions similar to their *Arabidopsis* counterparts (Yu et al., 1999).

The *AP1* and *AP3* genes are members of the MADS-box regulatory gene family (Riechmann & Meyerowitz, 1997). Members of this gene family are characterized by the presence of a highly conserved 57-amino acid MADS-box, which is also found in human (*SRF*), *Drosophila* (*MEF2C*), and yeast (*MCM1*) transcriptional activators (Purugganan et al., 1995; Riechmann & Meyerowitz, 1997; Alvarez-Buylla et al., 2000). Plant MADS-box genes also contain a moderately conserved 70-amino acid domain called the K-box, which is believed to possess the capacity to form coiled-coil structures. Two other regions (the I- and C-regions) are also found in the encoded proteins, but are poorly conserved in comparisons among different plant MADS-box genes (Purugganan et al., 1995; Riechmann & Meyerowitz, 1997). Functional studies of AP1 and AP3 proteins indicate that plant MADS-box proteins consist of two functional domains: (i) a core domain (MADS-box, I-region, and the 5′ portion of the K-box) involved in DNA-binding and dimerization functions, and (ii) a non-core domain (3′ end of the K-box and the C-region) that may function as the transcriptional activation domain (Riechmann et al., 1996; Krizek & Meyerowitz, 1996; Riechmann & Meyerowitz, 1997).

Recent evidence suggests that rapid morphological diversification in the silversword alliance has been accompanied by an accelerated rate of floral regulatory gene evolution (Barrier et al., 2001). Homologues to *AP1* and *AP3* (designated as *ASAP1* and *ASAP3/TM6*, respectively) have been isolated from developing flowers of *Argyroxiphium sandwicense* subsp. *macrocephalum*. Molecular phylogenetic analyses indicate that the *ASAP1* gene is an orthologue of the *Arabidopsis AP1* locus. The analyses further indicate that the *ASAP3/TM6* gene is a member of the *AP3* floral homeotic gene group, and appears to be an orthologue of the *Lycopersicon TM6* locus (Pnueli et al., 1991; Kramer et al., 1998). The *ASAP1* and *ASAP3/TM6* genes are present in duplicate copies (designated as the *A* and *B* copies, respectively) in the tetraploid Hawaiian species (Barrier et al., 1999), with both copies being transcriptionally active in developing heads (Barrier et al., 2001). By contrast, only single copies of the genes have been detected in North American tarweed species within the "Madia" lineage.

Molecular evolutionary analyses reveal that the *ASAP1* and *ASAP3/TM6* regulatory genes in species of the silversword alliance are evolving faster than their orthologues in the North American tarweed species (Barrier et al., 2001). Ratios of the number of nucleotide substitutions per nonsynonymous site to the number per synonymous site (or Ka/Ks ratios) in the coding regions of the genes are significantly higher among the Hawaiian species than among the North American species. For *ASAP1*, the mean Ka/Ks ratios are 0.98 ± 0.64 and 0.29 ± 0.12 for the Hawaiian and North American species, respectively. For *ASAP3/TM6*, the mean Ka/Ks ratios are 0.79 ± 0.52 and 0.12 ± 0.11 for the Hawaiian and North American species, respectively. (For both loci, the increases in Ka/Ks ratios among the Hawaiian species are significantly different from that expected by chance, as assessed by a bootstrap resampling test [$P < 0.001$].) Many of the pairwise interspecific Ka/Ks values for the *ASAP1* and *ASAP3/TM6* genes in the Hawaiian species are greater than 1, which suggests that positive selection and adaptive divergence may have operated to shape the structure of these transcriptional activators.

Unlike the floral regulatory genes, structural genes in the silversword alliance do not appear to exhibit substantially accelerated rates of evolution. For the *ASCAB9* structural gene, for example, the mean Ka/Ks ratios are 0.21 ± 0.30 and 0.14 ± 0.17 for the Hawaiian and North American species, respectively (Barrier et al., 2001). (The *ASCAB9* gene is an orthologue of the *Arabidopsis CHLOROPHYLL A/B BINDING PROTEIN9* photosynthetic structural gene.) The latter results are in general agreement with previous studies indicating limited genetic differentiation in structural allozyme loci among the Hawaiian species (Witter & Carr, 1988).

Species in the silversword alliance also exhibit variation in the *ASAP1* and *ASAP3/TM6* regulatory genes at the population level (Lawton-Rauh et al., 2003). Molecular population genetic analyses of the genes in *Argyroxiphium sandwicense* subsp. *macrocephalum* and *Dubautia ciliolata* subsp. *glutinosa* reveal significant levels of polymorphism in the introns, especially for the *ASAP1-A*, *ASAP1-B*, and *ASAP3/TM6-A* loci. Within the coding regions of

the loci, the type and distribution of polymorphic sites suggest a signature consistent with non-neutral protein evolution. Though polymorphism levels tend to be low in the coding regions, most coding region diversity occurs as nonsynonymous nucleotide substitutions in a majority of the loci. (Across all loci for the two species, there was a total of 14 nonsynonymous and only 3 synonymous substitutions.) The latter trend observed at the microevolutionary scale is consistent with the pattern observed at the macroevolutionary scale, as discussed above (Barrier et al., 2001).

Although the population-level patterning of polymorphic sites in the coding regions of the regulatory genes suggests the action of positive selection, statistical tests for selection cannot reject the possibility that the loci are evolving neutrally (Lawton-Rauh et al., 2003). Given the low number of polymorphic sites in the coding regions, the lack of detectable deviation from neutral-equilibrium expectations may not be surprising. With a low number of polymorphic sites, the commonly used tests for selection tend to have reduced power to reject neutral-equilibrium expectations. Further analyses should help to clarify the role that selective, demographic, and other forces play in shaping variation in the floral regulatory genes at the population level.

EVOLUTION OF GENES REGULATING VEGETATIVE DEVELOPMENT

A variety of genes affecting shoot growth and form have been identified in *Arabidopsis* and other species (Purugganan et al., 2003). Many of the genes encode transcriptional activators that directly regulate expression of downstream target genes. One group of growth regulatory genes includes *GA INSENSITIVE* (*GAI*) in *Arabidopsis* (Peng et al., 1997) and its homologues in various cereal grasses (Ivandic et al., 1999; Peng et al., 1999). These genes are a subset of the GRAS family of plant transcriptional activators (Pysh et al., 1999), and mutants are known to cause dwarfing in both monocots and dicots (Peng et al., 1999).

As candidate genes possibly involved in regulating vegetative development in the silversword alliance, *GAI* homologues (designated as *DaGAI*) have been isolated from leaves of the Hawaiian species (Remington & Purugganan, 2002). The *DaGAI* gene, like the *ASAP1* and *ASAP3/TM6* genes, is present in duplicate copies in the tetraploid Hawaiian species. The duplicate copies share conserved features that have been reported previously for the gene subfamily containing *GAI* and *RGA* from *Arabidopsis*, *d8* from *Zea*, and *SLR1* from *Oryza* L., including a conserved N-terminal DELLA domain (Peng et al., 1999; Remington & Purugganan, 2002).

Molecular evolutionary analyses indicate strong selective constraint in the coding regions of *DaGAI* in the Hawaiian species, although the constraint is somewhat relaxed in one of the two copies relative to *DaGAI* in North American tarweed species (Remington & Purugganan, 2002). There is also no strong evidence for positive selection on individual codons in *DaGAI*. Substantial variation exists, however, in the upstream flanking regions of *DaGAI* (Remington & Purugganan, 2002), including an elevated rate of nucleotide substitution in the middle upstream region. In addition, rates of nucleotide substitution and insertion/deletion (indel) appear to be decoupled to a large degree, as evidenced by comparison of the proximal and distal upstream regions. An overall decoupling is also apparent when the upstream flanking regions of the duplicate *A* and *B* copies of *DaGAI* in the Hawaiian species are compared, with the *B* copy having a similar number of nucleotide substitutions to the *A* copy but an elevated number of indels.

The results suggest that for *DaGAI* loci in the silversword alliance, positive selection may exert itself in the *cis*-regulatory promoter regions rather than in the protein-coding regions (Remington & Purugganan, 2002). Doebley and Lukens (1998) have proposed that variation in *cis*-regulatory regions of transcription factors may be a predominant mechanism by which novel variation in morphology arises, because transcription factors are often involved in coordinated regulation of specific developmental processes. Though no lines of evidence demonstrate positive selection to the exclusion of other possibilities for the Hawaiian *DaGAI* loci, the possibility of divergent selection in the upstream flanking regions is intriguing. In particular, some of the larger indels in the upstream flanking regions co-occur with major evolutionary transitions in growth form within the silversword alliance (Remington & Purugganan, 2002).

EPILOGUE

Regulatory gene evolution may thus play a key role in the adaptive radiation of the Hawaiian silversword alliance. In particular, the rapid and extensive diversification in reproductive and vegetative form may well be linked to alterations in the tempo and mode of evolution of the genes that control developmental processes. Additional analyses at macroevolutionary and microevolutionary scales

in the silversword alliance, and in other lineages undergoing adaptive radiation, should provide deeper insight into the genetic basis of morphological diversification, especially in reference to regulatory genes.

A more detailed understanding of adaptive radiation thus offers a special window into the evolution of life's diversity. Yet peering through this window is becoming ever more difficult, as the lineages undergoing adaptive radiation, especially those on oceanic archipelagos, suffer the impacts of habitat modification and loss and of alien species (Robichaux et al., 1998). The nature of the challenge is well-illustrated by the silversword alliance. Eight taxa in the silversword alliance (*Argyroxiphium sandwicense* subsp. *sandwicense*, *A. kauense* (Rock & M. Neal) O. Deg. & I. Deg., *Dubautia herbstobatae* G. D. Carr, *D. kenwoodii* G. D. Carr, *D. latifolia*, *D. pauciflorula*, *D. plantaginea* Gaudich. subsp. *humilis* G. D. Carr, and *Wilkesia hobdyi* H. St. John) are critically endangered. Thirteen additional taxa are rare or vulnerable (Wagner et al., 1999). The main threats confronting the taxa are competition by alien plants, predation by alien ungulates, and predation of pollinators by alien insects (Robichaux et al., 1998; Friar & Robichaux, 2003). Without a serious and sustained effort to eliminate the threats, and to reverse declines in distribution and abundance, many of the extant taxa will likely be lost to extinction, as has already happened in one case (*A. virescens* Hillebr.). A similar challenge also faces other lineages in Hawaii, such as the endemic honeycreepers and drosophilids, and on other oceanic archipelagos.

Thus, taking action now to prevent extinction is key to further exploring adaptive radiation and its link to genome evolution. Yet adaptive radiation also carries an important message for conservation (Robichaux et al., 1998). It serves to highlight that the biotic landscapes of Hawaii and other oceanic archipelagos are filled with dynamic, actively evolving lineages of plants, animals, and other organisms. Incorporating a lineage-based view into conservation planning, including the goal of providing opportunities for continued lineage diversification, may prove critical to long-term success.

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USING *MIMULUS* AS A MODEL SYSTEM TO UNDERSTAND THE ROLE OF INBREEDING IN CONSERVATION: GENETIC AND ECOLOGICAL APPROACHES[1]

Michele R. Dudash,[2] *Courtney J. Murren,*[2] *and David E. Carr*[3]

Abstract

In the preservation of plant biodiversity, there are fundamental genetic and ecological similarities involved in: (1) predicting the fate of small, isolated populations, (2) ensuring the successful reintroduction of endangered species back into natural habitats, and (3) understanding the establishment of species beyond their native ranges. In all three cases, populations small in size may experience high levels of inbreeding and subsequently the expression of inbreeding depression. The ability of these populations to persist will depend, in part, on the magnitude of inbreeding depression and the ability of selection to remove (or purge) the genetic load that causes inbreeding depression. The loss of genetic variation caused by inbreeding or drift in these small populations will restrict their evolutionary potential, placing a high premium on the ability of plants to respond plastically to environmental variation. When plants make appropriate phenotypic adjustments in truly novel environments while maintaining high fitness, we suggest the use of a new term, "opportunistic plasticity," for this attribute. Opportunistic plasticity may be particularly critical and advantageous in the case of plant introductions in ecological restoration where habitats resemble but are not identical to seed collection sites, or in the initial establishment phase of exotic species in non-native locations where many aspects of the environment differ from the native range. Overall phenotypic plasticity may also be an important means of dealing with environmental heterogeneity in many small populations, but unfortunately we have limited data on the interaction between inbreeding and plasticity in plants. The science and practice of conservation biology has generally appreciated the importance of inbreeding, but we feel that it will benefit greatly by considering the potential interactions between inbreeding and phenotypic plasticity and their effects in the establishment and persistence of small populations.

Key words: endangered species, inbreeding, inbreeding depression, invasive species, *Mimulus*, opportunistic plasticity, phenotypic plasticity, restoration.

A common ecological goal is the preservation of global biodiversity. The first urgent needs are habitat preservation and protection, followed by habitat restoration (e.g., Fenster & Dudash, 1994; Dudash & Fenster, 2000; Mack et al., 2000). To complement these fundamental first steps, we need creative, multifaceted research approaches that include basic biology, ecology, and genetics to provide informed predictions on how to preserve and hopefully restore native biodiversity (e.g., Dudash & Fenster, 2000; White & Boshier, 2000; Murren, 2002, 2003). Here we focus our discussion on the role of inbreeding and phenotypic plasticity in the conservation genetics of plants, and highlight the genetic and ecological obstacles facing small populations.

Newly established small populations of invasive exotics, small populations of rare plants, and new populations of native taxa utilized in restoration attempts share numerous genetic and ecological parameters (e.g., Holsinger, 1992; Adkison, 1995; Allendorf & Lundquist, 2003; Fig. 1). Genetic consequences of being in a small population potentially include inbreeding, low genetic diversity (which may represent only a subset of the genetic variation found in the entire species' range) (e.g., Nei et al., 1975; Barton & Charlesworth, 1984), limited gene flow among isolated populations (e.g., Groom, 1998; Parker & Haubensak, 2002), and rapid evolution via fixation of alleles through selection or genetic drift (Falk & Holsinger, 1991). Ecological challenges for the maintenance of repro-

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[2] Department of Biology, University of Maryland, College Park, Maryland 20742, U.S.A. mdudash@umd.edu

[3] University of Virginia, Blandy Experimental Farm, 400 Blandy Farm Lane, Boyce, Virginia 22620, U.S.A.

Figure 1. A flow chart that illustrates both ecological and genetic consequences of small populations following bottleneck. We draw attention to the parallelism in ecological and genetic obstacles of three conservation categories: locally rare or endangered species, invasive species, and restoration projects involving threatened or endangered species.

ductive success in small populations include attracting pollinators (Murren, 2002), selecting mates, attracting dispersal agents, and finding appropriate or open habitats for germination. Additionally, small populations must contend with both local natural and human-influenced environmental changes (e.g., Mack & Erneberg, 2002). In Figure 1 we outline the interactions between the genetic and ecological factors and how their relative importance will influence small population establishment, persistence, and risks of local population extinction (e.g., Sexton et al., 2002).

The phase in a small population's ecology on which we will focus here is the *initial* establishment, introduction, or colonization period (Williamson, 1996). In the areas of conservation and restoration, we advocate that initial colonization is a critical stage for which additional data are needed to effectively plan and manage species of concern (e.g., Elton, 1958). One ecological factor that may play an important role during the initial colonization phase of a population's history is phenotypic plasticity [changes in plant phenotypes in response to changing environmental conditions] (Schlichting & Pigliucci, 1998; Proffitt et al., 2003). Phenotypic plasticity may enable plants to respond to variation in abiotic and biotic regimes associated with their native environment and expand into new areas (Kaufman & Smouse, 2001).

Another biological process that lies at the intersection of ecology, genetics, and conservation is inbreeding, which may influence new population success as its effects vary among environments (e.g., Schemske, 1983; Dudash, 1990; Norman et al., 1995). Plants are unique in that many species are hermaphroditic and exhibit the potential to self-pollinate: approximately 70% of all species have selfing rates in excess of 20% (Vogler & Kalisz, 2001). Selfing is the most severe form of inbreeding because genetic heterozygosity is reduced by 50% with each generation of selfing (e.g., Charlesworth & Charlesworth, 1987). As it is likely that only a limited number of individuals colonize new habitats, relatedness among individuals within newly founded populations will increase quickly over the first few generations, making biparental inbreeding

(i.e., matings between relatives) likely. Biparental inbreeding reduces heterozygosity more slowly than selfing because relatedness is reduced (e.g., Ritland, 1989). Inbreeding creates two formidable challenges in the early establishment of populations. First, a common outcome is the manifestation of inbreeding depression in the resulting progeny (e.g., Charlesworth & Charlesworth, 1987). Second, inbreeding reduces the overall quantitative genetic variation and subsequently could reduce the ability of a population to respond to selection as well as reducing the mean population fitness. On the other hand, in small colonizing populations, inbreeding may confer important reproductive assurance when mates are scarce (Dole, 1992). There has been a tremendous amount of basic research on the effects of inbreeding but the links to conservation and management would benefit from further exploration of how these effects vary among environments (e.g., Keller et al., 1994; Mills & Smouse, 1994; Keller, 1998; Saccheri et al., 1998; Crnokrak & Roff, 1999). A novel next step would be to explore the interactions between inbreeding and phenotypic plasticity, which may be vital to making knowledgeable predictions as to which of the myriad of potential trajectories a given small population could follow in our human-altered global landscape.

The goal of this symposium contribution is both to review some of the ecological–genetic work to date on inbreeding and phenotypic plasticity in the model system *Mimulus guttatus* DC. (Scrophulariaceae) and use it as a starting point to illustrate how these data could be extended to inform conservation and restoration projects. In the opening section we will discuss results from fundamental biological studies on the genetic basis of inbreeding and suggest ways to incorporate knowledge about inbreeding into biodiversity preservation. How populations initially establish and persist in light of environmental changes *and* in the presence of inbreeding is the focus of the second section. Data on this interaction are rare at the moment, but we will review the pertinent work and propose a conceptual framework for future study. We will close by drawing attention to the need to explore this interaction between inbreeding and phenotypic plasticity to further our understanding of the management strategies required for small populations of invasive exotics, small populations of rare plants, and newly established populations utilized in restoration projects.

Model Organism in Evolutionary Ecology

Mimulus guttatus DC. (Scrophulariaceae, and recently assigned to the Phrymaceae; Beardsley & Olmstead, 2002) naturally occurs from Alaska to Mexico and is common in moist habitats throughout the western United States. Populations in the natural range are often spatially isolated and vary dramatically in size from very few plants to many thousands in one area (Vickery, 1974, 1999). From field observations, moisture appears to be a defining feature in the location of *M. guttatus* populations (Vickery, 1974). In its native range where moisture is seasonally ephemeral, *M. guttatus* acts as a common annual. However, in areas where water is continuously available particularly in coastal areas, perennial individuals can be found. *Mimulus guttatus* has naturalized in the eastern United States and Canada and around the globe in such localities as the British Isles, Western Europe, New Zealand, Tasmania, and Russia (Vickery, 1974).

Mimulus guttatus has large flowers that are visited by *Bombus, Apis mellifera, Dialictus,* and other small invertebrates in its native range (Dudash & Ritland, 1991; Gardner & Macnair, 2000). Often hundreds to thousands of seed per fruit are set. Seed dispersal by birds, wind, and stream transport suggest that continuous invasion or re-colonization of open patches and gene flow among patches occurs throughout the natural range of *M. guttatus* (Lindsay, 1964; Vickery, 1999). In natural drainages in Utah, Vickery (1999) demonstrated that over 30 years population sizes greatly fluctuate, local populations frequently go extinct, and populations re-appear at a variety of sizes. *Mimulus guttatus* also commonly exhibits opportunistic colonization, through seed dispersal by roadside mowing crews and other human-mediated influences. Individuals vary in many components of vegetative and life history traits in response to variable environments (Vickery, 1974, 1983; Galloway, 1995). Additionally, phenotypic plasticity may influence its success as a naturalized exotic in other portions of the globe as well as its success in native habitats.

The *Mimulus guttatus* complex is quite variable in its reproductive dynamics since many closely related sympatric species are able to mate successfully with each other in nature (Macnair & Cumbes, 1989). Members of the genus range from highly selfing to highly outcrossing (Vickery, 1964; Ritland & Ritland, 1989; Fenster et al., 1995). *Mimulus guttatus* has a mixed-mating system with population-level outcrossing rates estimated from allozymes ranging from 0.25 to 1.0 (Ritland, 1989, 1990; Dudash & Ritland, 1991; Willis, 1993b). Inbreeding depression in *Mimulus guttatus* was first noted by Darwin (1876), and many others have been inspired by his early observations of this phenomenon and

have built upon the growing knowledge of this taxon (e.g., Ritland & Ritland, 1989; Dole, 1992; Willis, 1993a, b; Fu & Ritland, 1994; Carr & Dudash, 1996, 1997; Carr et al., 1997; Dudash et al., 1997; Dudash & Carr, 1998; Willis, 1999a, b).

Inbreeding Depression and Its Genetic Basis

One enduring question related to understanding the enormous diversity among plant species is: Why do we observe selfing taxa evolving repeatedly throughout the plant kingdom (Stebbins, 1950; Grant, 1981)? The discourse surrounding this question has been primarily in the context of understanding how floral diversity in plants has evolved, as well as the evolution of plant mating and pollination systems, yet this topic has obvious links to conservation and restoration. The phenomenon of inbreeding depression, often quantified as the reduction in progeny fitness following selfing relative to progeny produced from random matings within a local population, is thought to be primarily responsible for the maintenance of outcrossing in most plant taxa (e.g., Charlesworth & Charlesworth, 1987), and is thought to potentially negatively influence populations of threatened or endangered species (e.g., Dudash & Fenster, 2000). However, following generations of selfing in the presence of inbreeding depression, a population may have purged or reduced its genetic load (eliminated deleterious or lethal alleles from the population), which may be a benefit to both endangered species and invasive taxa. Critical topics involving inbreeding that still need to be addressed in the area of conservation genetics include: (1) how inbreeding and subsequently inbreeding depression influence population establishment and persistence and, (2) whether populations can naturally purge their genetic load. The likelihood that a population is able to purge its genetic load is dependent on many factors, including the genetic basis of the inbreeding depression expressed, its mating system (outcrossing rate, t), abiotic and biotic selection pressures, conditional environmental effects, as well as genetic and structural incompatibilities associated with its breeding system.

Both genetic and ecological factors contribute to the prevalence of selfing species. If a plant species is able to mate with itself it provides reproductive assurance, i.e., independence from an external pollination agent for fruit and seed set (e.g., Schoen et al., 1996). The ability to self-pollinate increases the probability of survival at low population densities since pollinators may not be attracted to these small populations (e.g., Groom, 1998). Selfing permits a greater potential colonizing ability, since theoretically it could take just one individual to establish a new population or maintain an existing population across generations (e.g., Baker & Stebbins, 1965). Selfing contributes to local adaptation because of reduced pollen flow and subsequent localized seed dispersal (e.g., Antonovics, 1968). Selfing species may exhibit a lower cost of reproduction if cleistogamous flowers are smaller than chasmogamous flowers that are dependent on an external agent (e.g., Carr & Dudash, 1996), allowing selfing plants to shift resources that would normally go into larger flower production to another stage in their life history.

We have discussed many evolutionary advantages of selfing, raising the question of whether selfing is, in fact, an important ecological-genetic strategy for persistence of populations of small size. Inbreeding depression, however, can counteract both the ecological and genetic advantages to selfing in many plant taxa. Fisher (1941) first noted that when an individual in a population is able to readily both self and outcross, a selfing allele could invade an outcrossing population in the absence of inbreeding depression when ample pollen is also available to both self and outcross, i.e., pollen discounting (Nagylaki, 1976; Lloyd, 1979; Lande & Schemske, 1985). Models based on population-level inbreeding depression predict that if self progeny fitness is less than half of the fitness of outbred progeny (i.e., inbreeding depression $> 50\%$) a selfing allele cannot invade an outcrossing population (Charlesworth & Charlesworth, 1987). These theoretical arguments have been made at the population level; however, theoretical (e.g., Holsinger, 1991; Uyenoyama et al., 1993) and empirical work (e.g., Dudash et al., 1997) at the family level have demonstrated that a selfing allele may invade more easily through a population because of maternal line variation in inbreeding depression. Therefore, we recommend whenever possible that the assessment of inbreeding depression be done at both the family and population levels to provide more comprehensive insights into the inbreeding dynamics in the population of concern.

A population or family's ability to purge its genetic load is dependent upon both the presence of inbreeding depression *and* the genetic basis of the traits expressing the inbreeding depression. The genetic basis of inbreeding depression includes quantifying the number of contributing loci and the level of dominance of alleles at these loci. There are two genetic mechanisms thought to be responsible for inbreeding depression; however, they are not mutually exclusive (Charlesworth & Charlesworth,

1987). The first is dominance (or partial dominance)-based inbreeding depression in which loss of fitness is due to increased expression of recessive or partially recessive alleles as homozygosity increases (Wright, 1921). This type of inbreeding depression is maintained via a selection-mutation balance. Dominance-based inbreeding depression predicts that the frequencies of alleles that are strongly recessive and/or strongly deleterious will be greatly reduced by increased levels of selfing. On the other hand, equilibrium frequencies of more weakly recessive or mildly deleterious alleles will not be greatly affected by increased inbreeding. Selfing taxa are more likely than outcrossing taxa to purge their load if inbreeding depression is dominance based (e.g., Husband & Schemske, 1996; Dudash & Carr, 1998; Byers & Waller, 1999; Crnokrak & Barrett, 2002). Thus small populations that are primarily inbreeding have a greater probability of purging their genetic load, but their success will rest on whether the random changes in allele frequencies due to drift or the selective effects of purging prevail in the focal population. This combination of population attributes may further complicate the ability of small populations to cope with changing or unpredictable environmental regimes (but see below). In determining the role of inbreeding in conservation, an understanding of the genetic basis of inbreeding depression better enables one to predict the breadth of potential outcomes of a conservation breeding-program and provides additional insights for risk assessment models.

The second genetic mechanism thought to be responsible for the expression of inbreeding depression is overdominance or heterozygote advantage, where the heterozygote is more fit than either homozygote (Charlesworth & Charlesworth, 1987; Uyenoyama & Waller, 1991). Heterozygote advantage in this case is thought to be maintained by balancing selection. Since heterozygotes do not breed true, inferior homozygote genotypes are produced each generation, and these homozygotes will reduce the overall population fitness (i.e., segregational load). With overdominance there are no expected differences in a population's ability to purge its genetic load based on population size or mating system (selfing vs. outcrossing). However, because of the increased role of genetic drift relative to selection in small populations, we do not expect to observe the maintenance of polymorphisms at overdominant loci, which would reduce mean population fitness. Furthermore, a reduced ability of natural selection to offset the effects of genetic drift will also make it more difficult for small populations to respond to changing environmental regimes via genetic variation alone.

In conservation genetics, knowledge of the mating system of the taxon of concern is required to effectively conduct a breeding program via hand-pollinations that produces the greatest amount of viable seed. Decreases in population size promote biparental inbreeding and often selfing, but will these shifts in mating opportunities result in a purging of the genetic load? Recent detailed reviews of the genetic basis of inbreeding depression in plants support the prevalence of dominance-based inbreeding depression (e.g., Husband & Schemske, 1996; Carr & Dudash, 2003). However, there has been some debate on the relative importance of purging in natural populations (see Byers & Waller, 1999; Crnokrak & Barrett, 2002). The debate has been fueled in part by the plethora of approaches (e.g., hand-pollination experiments vs. related selfing and outcrossing taxa assessments, variation in traits quantified, attempts at generalities among taxa) used to assess purging and the omission of important ecological and genetic parameters that will influence the likelihood of purging.

Inbreeding: Insights for Conservation

The role of inbreeding and the likelihood of purging in small populations of conservation concern are central to understanding long-term population dynamics. In restoration attempts, one might undermine local population success by utilizing close relatives that subsequently inbreed, and compromise their ability to maximally reproduce. In fragmented habitats with isolated small populations of threatened species, we are concerned with whether inbreeding may reduce seed output, and we frequently debate whether it is necessary to import pollen from other distant populations. It is also well known that one can invoke the expression of outbreeding depression following hand long-distance crosses between two populations, which results in a reduction in progeny performance and vigor, further compromising the population of concern in the long-term (e.g., Fenster & Galloway, 2000). Monitoring invasive taxa at the initial colonization event may allow a unique opportunity to directly observe a suite of traits and how they vary among individuals that together promote a successful invasion into a non-native habitat. All of the management situations mentioned above would benefit from knowledge of the mating system (who mates with whom) and breeding system (morphological and temporal variation both within and among flowers on a plant) of the taxa of concern.

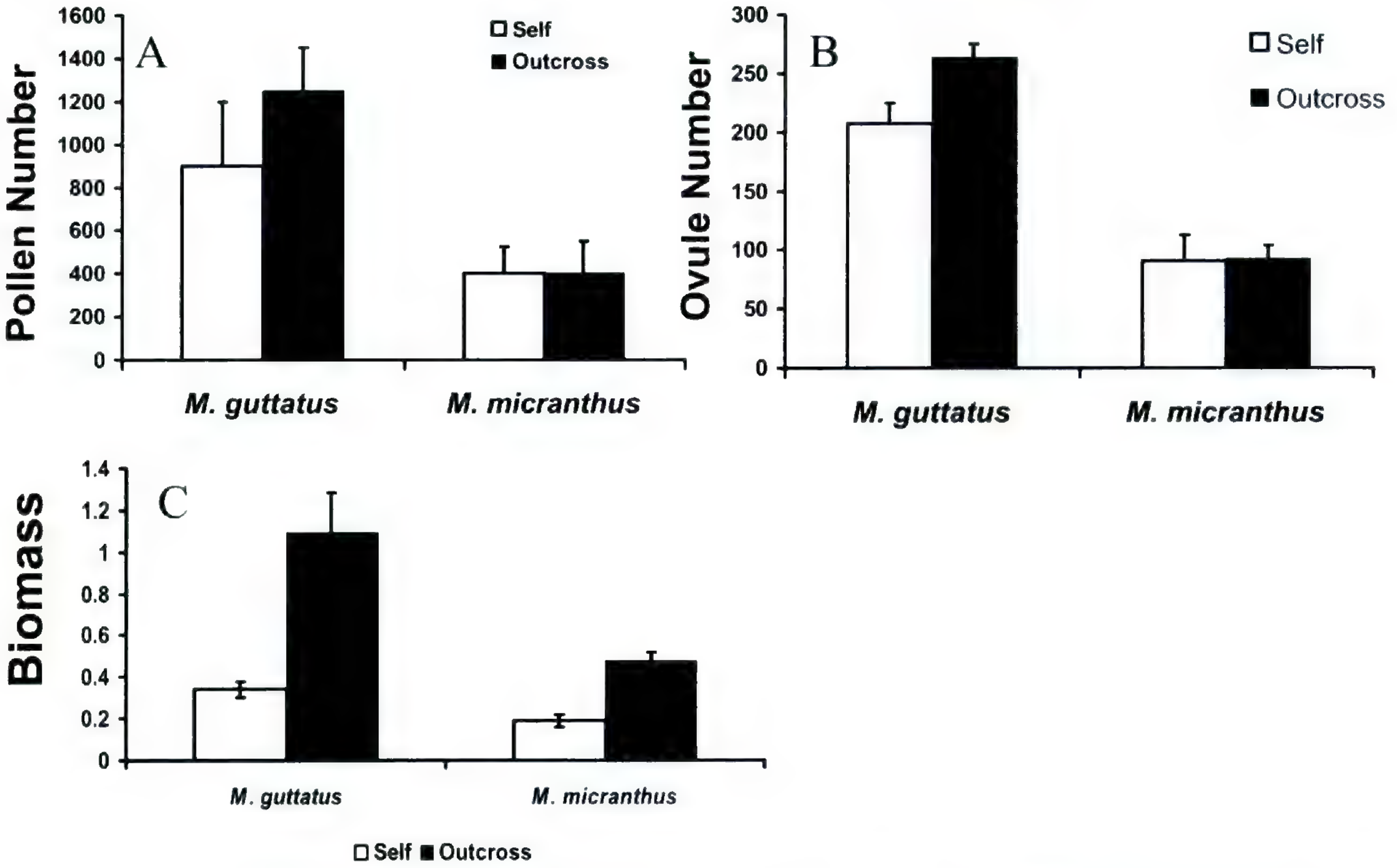

Figure 2. Comparison of progeny performance in the glasshouse following one generation of selfing and outcrossing populations in both *Mimulus guttatus* and *M. micranthus*.—A. Pollen production. —B. Ovule production. —C. Above-ground biomass. The 95% confidence intervals (indicated by vertical lines) on all three panels reflect the variation among maternal families.

By examining the relationship between the plant mating system and the expression of inbreeding depression whenever possible, we can begin to build predictions of which taxa will be more vulnerable to the consequences of small population size. To this end, we assessed whether natural selection was more effective in purging the genetic load of the selfing *M. micranthus* A. Heller versus the mixed-mating *M. guttatus*. *Mimulus micranthus* is a strict annual that produces flowers that are three to four times smaller than *M. guttatus*. This taxon has a distribution limited to the coastal range of central California, but is often found sympatrically with *M. guttatus*. Furthermore, we quantified the stage and magnitude of inbreeding depression expressed in the progeny after performing hand-self and outcross pollinations in the glasshouse. The mixed-mating *M. guttatus* progeny demonstrated significantly greater inbreeding depression in adult above-ground biomass, ovule production, and pollen production per flower than the progeny of selfing *M. micranthus* (Carr & Dudash, 1996; Fig. 2A, B, C). *Mimulus micranthus* self progeny (Fig. 2A, B, C) exhibited significant inbreeding depression in adult above-ground biomass compared to their companion outcrossed progeny (Fig. 2C), but no inbreeding depression for either pollen or ovule production per flower, two traits closely linked to fitness (Fig. 2A, B). Overall it appears that many uncorrelated loci of small effect are responsible for inbreeding depression in both species (Carr & Dudash, 1997; Dudash et al., 1997; Dudash & Carr, 1998). As theory predicts when assuming dominance-based inbreeding depression, the magnitude of inbreeding depression when present was much greater in the mixed-mating taxon versus the selfing taxon. Additionally, purging of genetic load for pollen and ovule production in the selfing taxon has been much more efficient through its mating system.

Our work and that of others (e.g., Husband & Schemske, 1996) demonstrate the important role of mating system in the opportunity to purge genetic load. Quantifying the mating system (using allozymes if plant tissue and funds are available) as well as breeding system (using detailed field observations to determine the timing of pollen dehiscence, stigma receptivity, whether the plant is monoecious, dioecious, etc., degree of herkogamy or dichogamy of perfect flowers, and overall floral display) would be helpful as a first approximation of the likelihood that a species may be capable of purging its genetic load. For example, if a taxon of concern readily self-pollinates, it may naturally have a reduced genetic load and may be an excel-

lent candidate to use in a restoration effort; its reproductive assurance mechanism increases the chances of success of the project. On the other hand, the reintroduction or establishment of a typically outcrossing species may require a much greater propagule number in order to minimize the likelihood of matings between relatives and any subsequent expression of inbreeding depression. These scenarios call attention to the importance of knowing the reproductive biology of organisms slated for conservation management initiatives.

An approach that has been utilized in designing some conservation efforts of endangered species is hand-pollination experiments to artificially inbreed a taxon in an attempt to reduce its genetic load (e.g., Hedrick, 1994; Kalinowski et al., 2000). We performed this approach for two populations of the mixed-mating *M. guttatus* to examine how the expression of inbreeding depression varied among traits, maternal lines, and between populations, across five generations of serial inbreeding and outcrossing. The crossing program revealed that the magnitude of inbreeding depression was relatively constant in both populations for total flower production, adult above-ground biomass, and pollen and ovule production (Carr & Dudash, 1997; Dudash et al., 1997). At the population level, our results were consistent with dominance-based inbreeding depression with weak selection on partially deleterious alleles; however, we could not rule out overdominance. At the family level, maternal lines varied dramatically in their responses in their trait expression: some increased, some decreased, and some were unaffected by inbreeding. The families that exhibited purging of their genetic load (reflected by the inbred lines outperforming the outcrossed lines) also suggest dominance-based inbreeding depression. However, whether weak selection or drift was responsible for the increased fitness is not known, and both may play important roles in nature. In a greenhouse study Willis (1999b) enforced strong selection by serial inbreeding 1200 maternal lines and saw great improvement in inbred performance of many maternal lines relative to outcrossed relatives, again suggesting evidence of purging. Small populations, such as the experimental populations described above, are prone to genetic drift; therefore the fixation of alleles may have either positive or negative effects on overall fitness. Many conservation efforts would benefit greatly by gathering data on inbreeding depression to assess the consequences of long-term persistence at small population sizes across generations. However, it is not necessarily practical for many threatened species; therefore, extrapolation from other native species may be warranted.

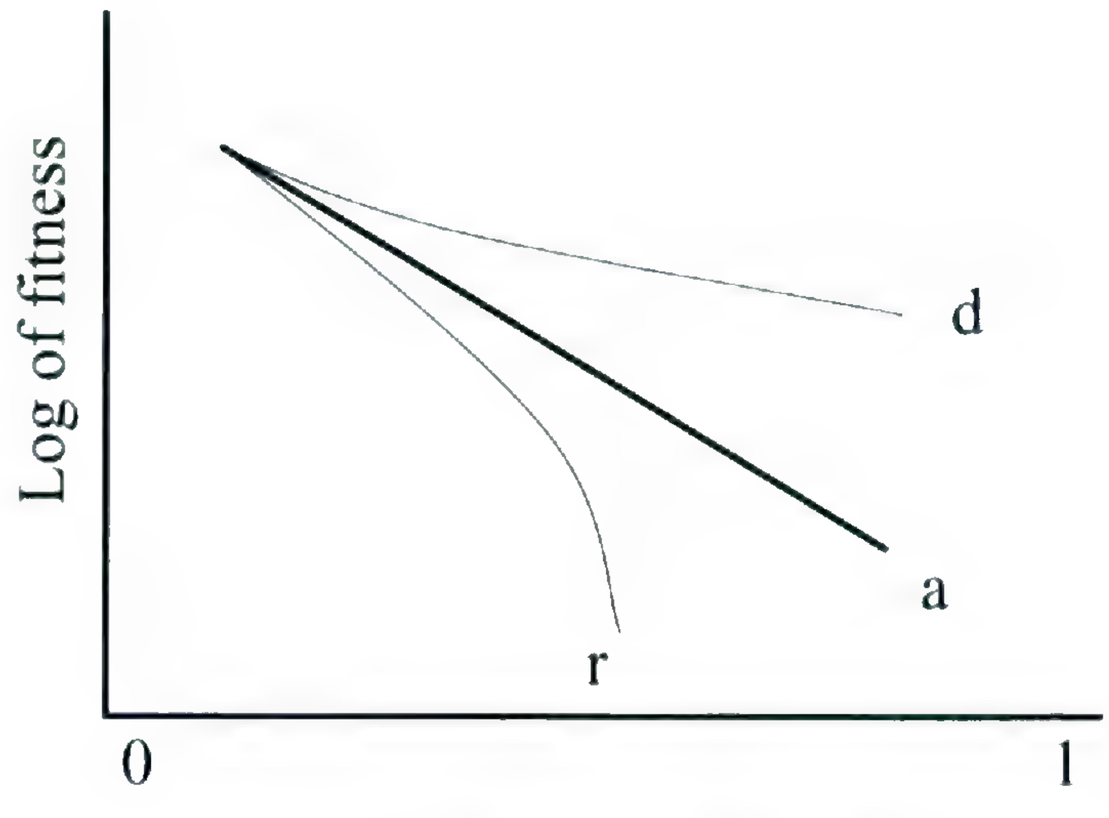

Figure 3. Logarithmic relationship of inbreeding level and fitness, with and without epistasis. Inbreeding level ranges from zero to one, with one being completely inbred. Letter **a** denotes a log-linear relationship, in the absence of epistasis, where the effect of homozygosity at a given locus is independent of the genotype at other loci. Letter **d** describes diminishing epistasis, where the interactions among loci are non-independent, making the slope of the relationship between inbreeding and fitness more shallow. Letter **r** describes reinforcing epistasis where interactions among loci are non-independent, making the slope of the relationship between inbreeding and fitness drop off sharply at intermediate levels of inbreeding. Extending this graph across environments may be an important exercise for predicting the maintenance of fitness of species of conservation concern.

Variation among maternal lines provides: (1) a mechanism for the invasion of a selfing variant into an outcrossing population (Holsinger, 1991; Dudash et al., 1997), or (2) the maintenance of genetic variation among different maternal lines in alternate homozygous states. This variation can be produced from random differences in the distribution of deleterious mutations (Schultz & Willis, 1995), prior history of inbreeding (Uyenoyama & Waller, 1991), and also by epistatic interactions among loci (Goodnight, 1999). In our experiments we detected evidence of epistasis (intergenic interactions) at the maternal family level but not at the population level (Dudash et al., 1997). The data suggest diminishing epistasis, which by definition slows down the purging of genetic load, i.e., the maintenance of fitness as inbreeding increases (Fig. 3). These results have implications for breeding programs of endangered or threatened species because enforced selfing may *not* purge the genetic load in a linear fashion if maternal line variation and epistasis inhibit the purging process (Fig. 3). The presence of epistasis makes it even more difficult to readily estimate the

likelihood of purging in conservation breeding programs (Fenster et al., 1997; Fenster & Galloway, 2000). Caution should be exhibited by all researchers attempting to enforce purging as a mechanism of preserving quantitative genetic diversity of species of conservation concern.

Overdominance could not be excluded as a possible explanation for some of the patterns that we observed in our comparisons of *M. guttatus* and *M. micranthus* and the population level behavior of our inbred lines of *M. guttatus*. We therefore sought further evidence that selection was acting against recessive deleterious alleles (dominance-based inbreeding depression) with a more direct estimate of dominance from a North Carolina III quantitative genetics design (Comstock & Robinson, 1952). We showed both above-ground biomass and total flower production in *M. micranthus* were more nearly additive and expressed less dominance-based inbreeding depression than in *M. guttatus*. We directly confirmed theoretical predictions that purging had been more efficient in the selfing taxon. The significance of these results for conservation is that both indirect estimates described above and the direct estimate from the North Carolina III breeding design were consistent in demonstrating evidence for dominance-based inbreeding depression. We do not recommend replication of the North Carolina III breeding design (Comstock & Robinson, 1952) for target conservation species because of the need for a large number of individuals, the use of inbred lines, and the extensive time required to conduct the experiment. Nevertheless, we can utilize the inferences made from model systems to make knowledgeable predictions for conservation. Therefore, the numerous indirect estimates of inbreeding depression and the likelihood of purging that have been the model for native plant species can be utilized to build management plans.

In all the experiments that we have described above, maternal line variation was a critical source of genetic variation. We consider this to be an important observation that should be kept in mind when collecting seed in the field for germplasm databases. We suggest that maternal lines should be kept separate instead of bulk collected for use in breeding programs to enhance or maintain genetic diversity for restoration projects. Conservation efforts for invasive species warrant *aggressive removal of small populations* as soon as they are detected (e.g., Simberloff, 1997; Farnsworth & Ellis, 2001), as any observed maternal lines are likely those that are successful in the novel environment and may have overcome the effects of inbreeding depression, perhaps via purging. Prior to the impending population explosion of the non-native plants, this is the stage where control efforts may actually make a huge difference, and we consider this management practice to be under-utilized.

A notable result of direct relevance to conservation initiatives involving breeding programs is that the process of generating inbred lines of *M. guttatus* reduced the number of original maternal lines by 50% (Dudash et al., 1997). This dramatic loss of lines is an important warning when designing a hand-pollination breeding design in the greenhouse or in situ hand-pollination plan for viable seed generation for plant taxa of conservation concern for which little seed is available. A breeding design with the intent of reducing the genetic load may result in the loss of important genetic variation through the extinction of maternal lines, from male sterility or loss of seed viability, owing to the exposure of homozygous recessive lethals or partial lethals (Dudash et al., 1997; Dudash & Carr, 1998; Willis, 1999a, b; Hedrick & Kalinowski, 2000). On the other hand, for invasive species a history of purging, or purging following initial establishment, or the expression of non-additive genetic effects (e.g., epistasis) may contribute to success in a novel environment.

Data on inbreeding depression are often generated in the glasshouse environment, which is known to minimize the effects of inbreeding (e.g., Schemske, 1983; Dudash, 1990; Norman et al., 1995). We advocate that the quantification of inbreeding depression be done in the field whenever possible, and to test whether purging in nature occurs at a much slower rate across many generations than the serial inbreeding approach commonly used in greenhouse experiments. Different genetic mechanisms and interactions may be occurring to either enhance or inhibit the efficacy of purging. We reemphasize the importance of maternal line variation discussed above, although our *M. guttatus* data were all collected in a controlled greenhouse environment. Patterns of variation among maternal families observed in the greenhouse may be significantly altered when environmental heterogeneity is experienced in the field in native and non-native habitats. As conservation efforts are focused in field settings, the exploration of the interactions between maternal line variation and habitat heterogeneity are vital data to collect (see Mazer & Lebuhn, 1999).

Phenotypic Plasticity

Together with inbreeding, changes in the environment may dramatically influence the probability

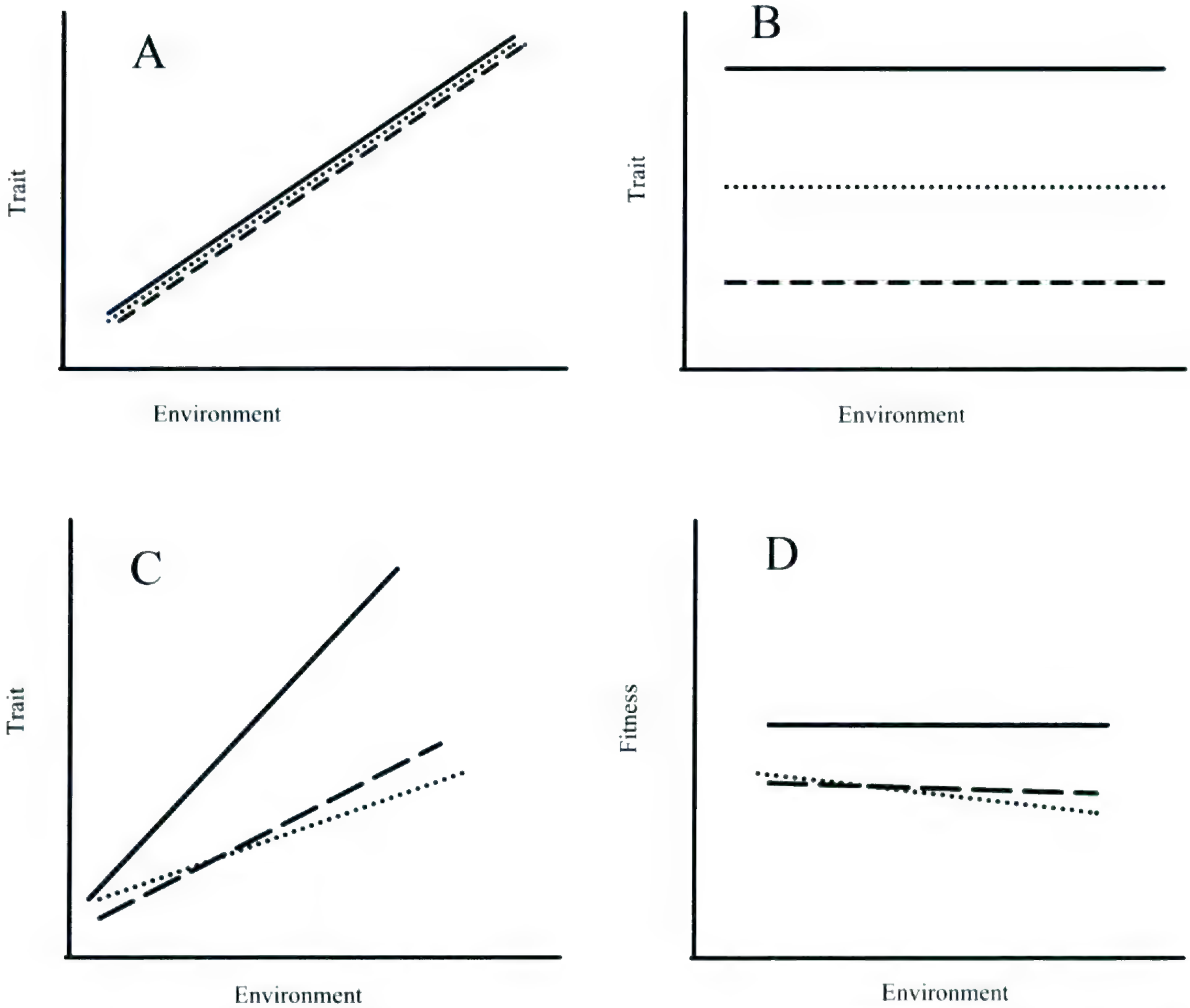

Figure 4. Each line represents a genetic unit (genotype, family, or population: depending on the level of analysis). —A. All three genotypes respond in the same way to the environmental gradient, thus all genotypes are plastic (significant treatment main effect in ANOVA model). —B. All genotypes have flat reaction norms, in other words, they are not plastic because they do not respond to the environmental gradient. However, the genotypes do differ in their mean trait response (significant genotype, family or population main effect in ANOVA model). —C. This is a common reaction norm diagram. All three genotypes are responding differently to the environmental gradient by both changes in slope and changes in rank order of genotypes from one environment to another (crossing reaction norms). This indicates plasticity (trait value is higher as environmental unit increases) and genotype by environment interactions. (Significant effects in ANOVA model, treatment, treatment*genotype, and genotype.)—D. This panel is different in that now the Y-axis represents fitness (fitness reaction norm). Two genotypes have flat reaction norms for fitness (solid and dashed line). The genotype with the dotted line is plastic for fitness. *It is important to note that the solid and dashed line genotypes may be plastic for morphological, physiological, life history, and other traits, which may contribute to the maintenance of a flat reaction norm for fitness.* If this is the case, then genotypes represented by the solid line and dashed line may be indicative of adaptive phenotypic plasticity.

of small population establishment and subsequent persistence of threatened and endangered species as well as newly established populations of non-native taxa. How a genotype alters or maintains its phenotype in response to a range of environments can be explored graphically by examining patterns of a reaction norm diagram (see Fig. 4 for an explanation of common patterns). The maintenance of a phenotype by a genotype across environmental gradients describes a non-plastic genotype for the phenotypic trait of interest (a flat reaction norm), whereas a plastic response is characterized by variation in the phenotype across environments (a sloped reaction norm).

Examining the reaction norm diagrams for fitness-related traits together with the patterns of plasticity of other phenotypic traits may suggest how plasticity of other phenotypic traits influences fitness across environments. Adaptive phenotypic plasticity describes the capability of organisms to maintain high fitness across different native environmental conditions by exhibiting plasticity in oth-

er non-fitness traits (which broadly include morphological, architectural, anatomical, physiological, behavioral, and life history traits, all of which can vary across development) in response to environmental heterogeneity (Sultan, 1995; Pigliucci, 2001). Because selection favors high fitness of genotypes in all environments, it will also favor plastic responses of non-fitness traits across environments that achieve this fitness effect. However, phenotypic changes may not be sufficient to adequately buffer against environmental changes, leading to variation in fitness levels across environments (Schlichting & Pigliucci, 1998). Different genotypes or different populations may respond plastically to the environmental gradient by changing *alternative* quantitative traits (e.g., leaf size, time to flowering, number of branches, leaf thickening) to maintain or maximize fitness (Marshall et al., 1986; Sandquist & Ehleringer, 1997; Ottenheim et al., 1998; Sultan et al., 1998). The correlations of reaction norms of vegetative and fitness traits may suggest adaptive phenotypic plasticity; however, explicit tests are required to confirm the hypothesis (Schlichting & Pigliucci, 1998).

We predict that small populations, which express genetic variation for plasticity, may increase their chances of survival in light of human disturbance of native habitats (Fischer et al., 2000; Paschke et al., 2003). Similar patterns to those described above might be observed for invasive species outside their native range or for populations established as restoration projects in putative suitable habitats (e.g., Schweitzer & Larson, 1999). In these cases, as selection may or may not have had time to directly shape these responses in the novel non-native or previously unoccupied environment (Mack et al., 2000; Heath et al., 2003), we suggest that the term adaptive phenotypic plasticity may not be entirely appropriate. Instead, here, we coin a new term, *opportunistic plasticity.*

We define *opportunistic phenotypic plasticity* as (1) the maintenance of fitness across the heterogeneous habitats of the novel environment, or (2) the increase in fitness when moving from the native to non-native environment, through the modification of non-fitness traits (e.g., vegetative and life history characters). In the case of invasive taxa, we predict that mean performance frequently will increase in the novel environment in comparison to the native environment (Fig. 5), associated with ecological release from predators, parasites, herbivores, competitors, etc., of the native habitat (e.g., Williamson, 1996; Keane & Crawley, 2002; Quinn & Wetherington, 2002; Conner et al., 2003), as resources can be reallocated to optimize growth and reproduction.

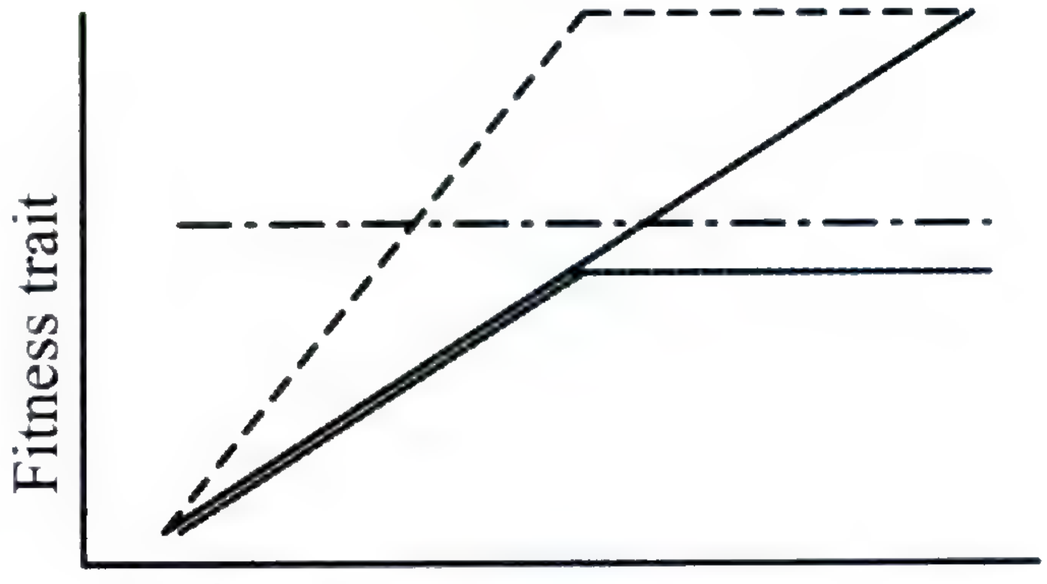

Figure 5. Fitness-related traits in response to environmental variation. The graph illustrates the transition from native to novel environments, and two different habitats in the novel environment. We characterize several potential fitness responses that may be expressed by invasive taxa. The dash-dot line represents a genotype that expresses no variation in fitness-related traits across environments. The solid line represents a genotype that shows a linear increase in fitness across environments. The dotted line represents a genotype that shows a marked increase from native to novel environments, but a flat reaction norm to fitness across the novel environments. The dashed line shows a similar pattern for the genotype as the dotted line genotype, with the exception that the plasticity of fitness is much greater in the initial transition from native to novel environment.

In other words, we consider plasticity *opportunistic* when initial colonists are not adapted to these novel conditions, yet their subsequent generations could become adapted as selection and drift operate in the *new* environment. Opportunistic plasticity as defined here may play an important role in the establishment and persistence of new populations.

Hidden Reaction Norms

Invasive species may express phenotypic plasticity of a multiplicity of traits in response to the new environmental conditions of their non-native range to maximize fitness. The response to novel environments may represent an extension of the responses to environmental conditions experienced in their native environment, particularly if there are similarities among habitat characteristics and gradients between the native and non-native environment (Schlichting & Pigliucci, 1998; Schlichting & Smith, 2002; Schlichting, 2003, 2004; Schlichting & Murren, 2004; Fig. 6). On the other hand, completely different reaction norms could be uncovered (Schlichting, 2003, 2004). Examining phenotypes or phenotypic responses only in the native range may limit our ability to predict vegetative and fitness-related responses to non-native environments.

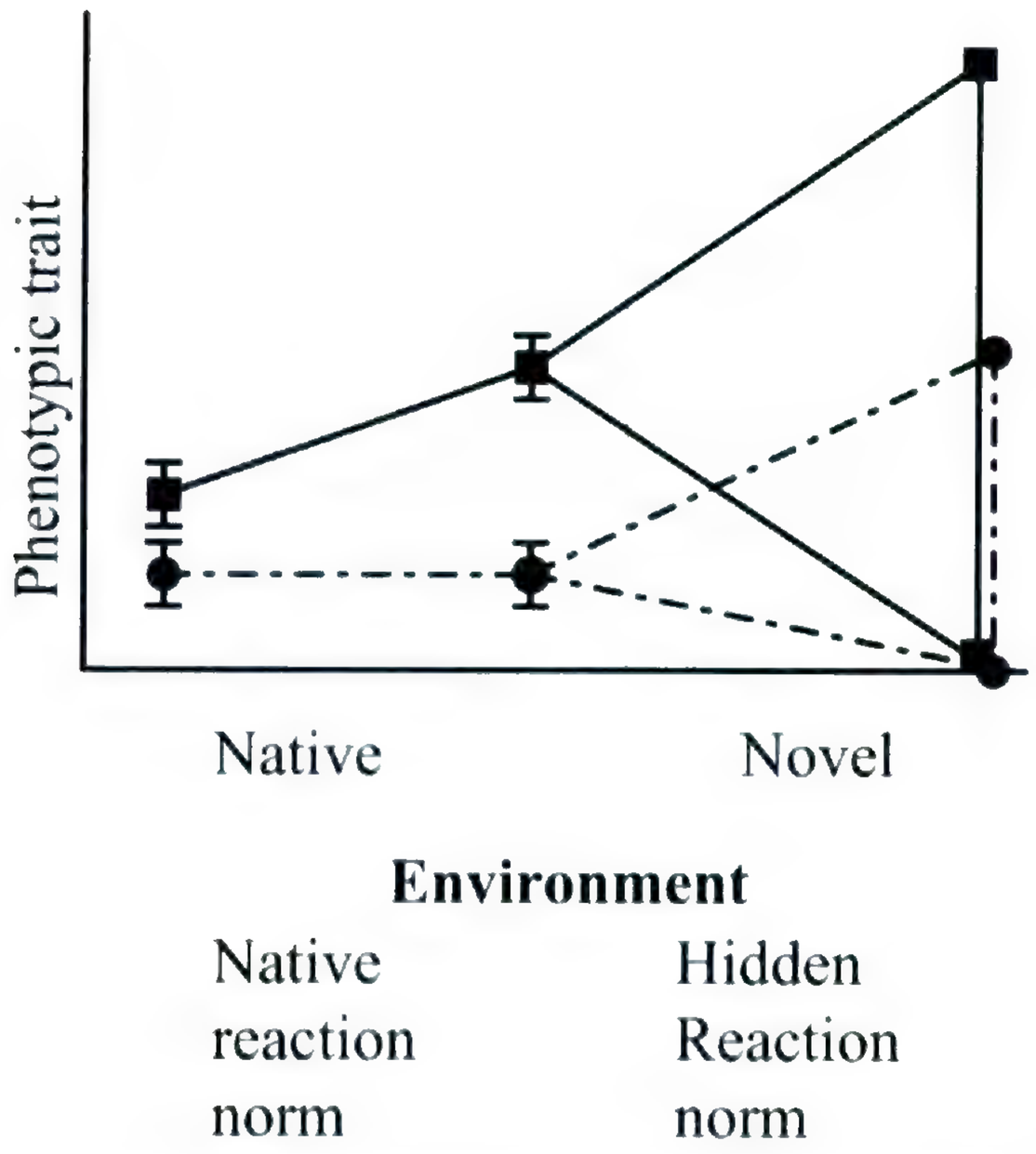

Figure 6. A conceptual hidden reaction norm diagram of a phenotypic trait across two native and one novel environment. The vertical dotted line demarcates the transition from native to novel environments. Here we illustrate two genotypes. The dash-dot line genotype has a flat and canalized (represented by tiny error bars around trait means) reaction norm in the native environment. The solid-line genotype has a plastic and canalized reaction norm in the native environment. For both genotypes, the response to the novel environment may not be predictable given the shape of the reaction norm in the native environment. In both cases, the trait value can increase, decrease, or remain the same. The varieties of potential responses are indicated through triangles across the transition from the native to the novel environment.

For example, novel patterns of phenotypic plasticity may be expressed in the new environment associated with the non-native geographic location (Fig. 6). Many studies that examine plasticity under stressful or novel environmental conditions have shown that the phenotypic variance around a trait mean is increased in the new environment, in comparison with the native environment (e.g., Windig et al., 1994; Holloway et al., 1997). Uncovering these hidden reaction norms (Schlichting & Pigliucci, 1998; Schlichting & Smith, 2002; Schlichting, 2003, 2004; Schlichting & Murren, 2004) could reveal a potential storehouse of genetic and phenotypic variation that could be selected upon and expressed in the new geographic location (Fig. 6).

In regard to invasive species and traits associated with invasion success, examination of genetic variation for plasticity has just begun. We will briefly discuss a few published examples of invasives, while keeping in mind that the same issues may be relevant for restoration projects (e.g., Montalvo & Ellstrand, 2000), where we are not aware of any studies where plasticity has been explicitly quantified. In some cases invasives may have more rapid growth rates, express physiological plasticity (e.g., Baruch et al., 2000), or may be superior competitors in low-nutrient conditions (e.g., Milberg et al., 1999). Population persistence of an invasive species necessitates that the individuals exhibit phenotypic responses appropriate to novel environmental attributes in the non-native range. For example, Byers and Quinn (1998) compared responses in demographic and reproductive characteristics of *Alliaria petiolata* (M. Bieb.) Cavara & Grande (garlic mustard, Brassicaceae) to four microhabitats in an invasive location. They conclude that although survivorship differed among habitats, there is a positive correlation between the observed phenotypic variation in demographic and reproductive characteristics and success in the novel environment (see also: Luken & Goessling, 1995; Stewart & Potvin, 1996; Kaufman & Smouse, 2001; Stratton & Goldstein, 2001). These studies serve as a starting point to understand the relative importance of genotype by environment interactions for particular traits that may act as vital predictors of invasiveness.

Returning to the model organism, *Mimulus guttatus*, genetic variation for phenotypic plasticity is known to be present for several vegetative and life history traits from glasshouse and field experiments (Vickery, 1974, 1983; Galloway, 1995). The presence of phenotypic variation in the field persuaded Vickery (1974) to test whether tolerance to a broad range of temperatures and light intensities might contribute to the success of *M. guttatus* in colonizing a wide variety of habitats in native and non-native locations. Vickery studied an array of native populations, which originated from Alaska south to Utah, and exposed them to combinations of light and temperature treatments reflecting their range in natural environments. Vickery found significant variation in responses to artificial temperature environments among clones of different populations and among genotypes within populations for plant height, plant dry weight, days to first flower, leaf length and width, and node of first flower. Overall, plants at the extreme temperatures were smallest. Increased light availability resulted in significant increases in plant biomass and flower production. Vickery's graphs provide evidence for genotype by environment interactions (see Fig. 7 drawn from data in Vickery, 1974). Yet, Vickery did not find direct concordance between their optimal growth conditions in the glasshouse and their native con-

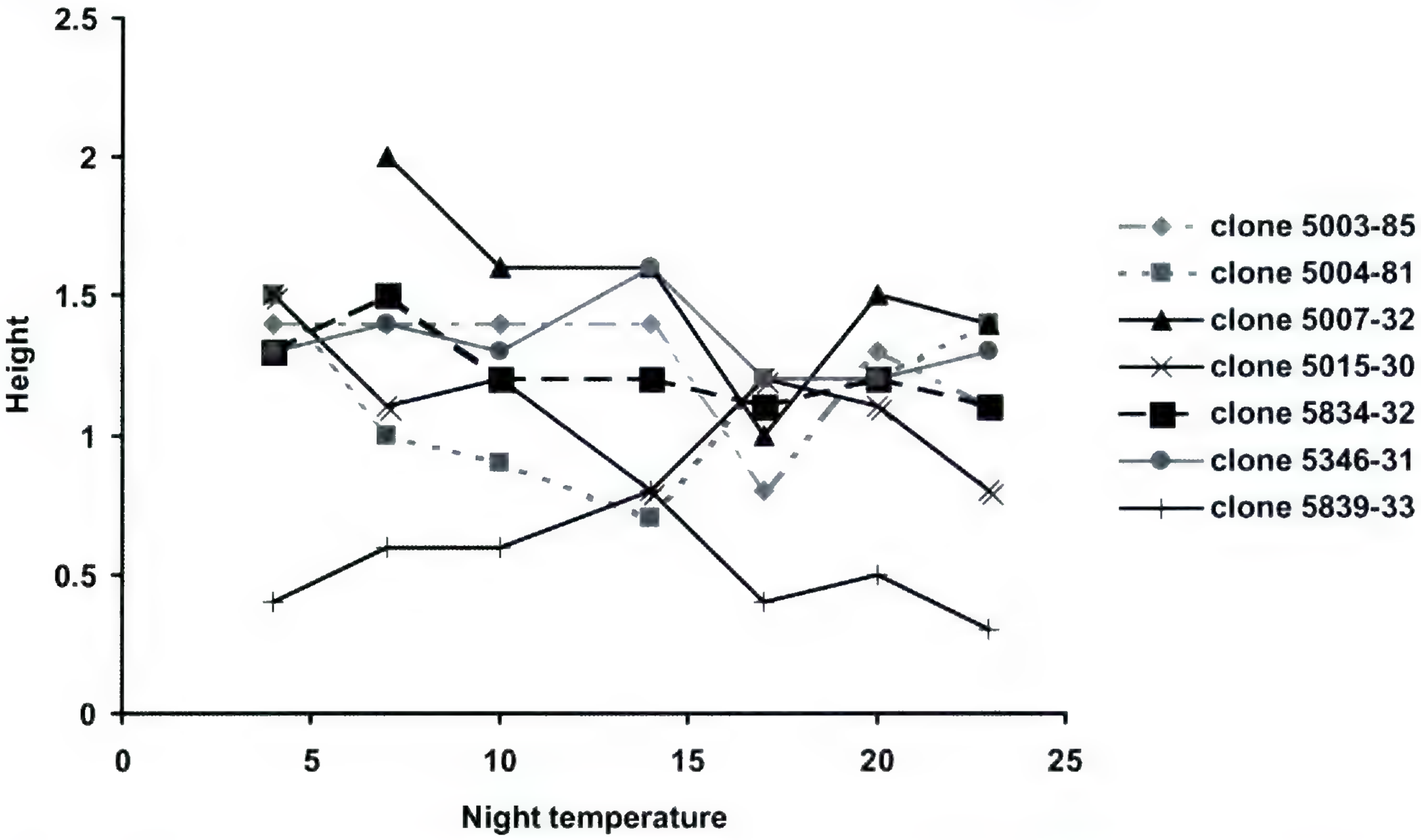

Figure 7. The reaction norms of seven *Mimulus guttatus* clones from different geographic areas drawn from data in Vickery (1974). The height of each clone was measured in seven night temperature environments. The diagram depicts phenotypic plasticity, genotype by environment interactions, and genetic variation for height within environments. What is not shown on this diagram but reported by Vickery (1974) is that optimal fitness and non-fitness trait expression does not necessarily correspond to the home environmental conditions.

ditions. Several cloned genotypes of *M. guttatus* showed both the maintenance of seed production across environmental treatments and plasticity of vegetative traits. These two components provide evidence for the expression of opportunistic plasticity of this species. Since these populations often grew best in conditions outside their native habitat, Vickery concluded that these responses might contribute to the success of *M. guttatus* as a colonist both in its native habitat and in non-native habitats. Observation of patterns such as these in other species could be used as evidence to predict colonization success, persistence, and expansion of populations outside their native range and may serve as an indicator of invasive potential.

Galloway (1995) examined phenotypic plasticity of *M. guttatus* in naturally heterogeneous field conditions using clonally propagated individuals, and found significant genotype by environment interactions for a number of traits. She went on to demonstrate that maternal environment affected the strength of genotype by environment interactions of the offspring in two ways: (1) greater mean flower production and less plasticity for vegetative traits in the offspring of maternal plants from more stressful sites, and, in contrast, (2) decreased flower production and greater plasticity in a variety of vegetative traits in the offspring of maternal plants from less stressful sites. These data are evidence that maternal effects, genotype by environment interactions, and environmental variation at macro and micro scales contribute to the maintenance of genetic variation for vegetative and life history characters and their plasticities in populations of this species. This study illustrates the importance of collecting data on habitat heterogeneity and genetic variation of seed source populations, and such data could serve as indicators of which populations may be successful in novel environments.

Linking Inbreeding and Phenotypic Plasticity in Conservation

Very few researchers have explored the link between inbreeding and phenotypic plasticity within the basic research arena; therefore, we have limited predictions of how these two important ecological and genetic phenomena interact and influence a population's evolutionary trajectory (Lewis, 1954; Pederson, 1968; Schlichting & Levin, 1986). Are phenotypic plasticity and inbreeding positively correlated, negatively correlated, or not correlated at all? And if correlated, are fitness-related traits positively or negatively impacted? We contend that in-

dependently both inbreeding and phenotypic plasticity have important implications for conservation as we have discussed above. Furthermore, the interaction between inbreeding and phenotypic plasticity may directly impact whether small populations are maintained, whether new small populations successfully establish, and whether these new populations persist. Thus understanding the interaction between inbreeding and phenotypic plasticity has the potential of providing important insights into conservation and management of threatened or endangered species, restoration projects of species of concern, and invasive species (e.g., Quinn & Wetherington, 2002).

We are aware of a few published studies that directly examined plasticity of vegetative traits among inbred and outcrossed lines. Earlier work on *Lycopersicon* (*Solanum* in Solanaceae) and *Arabidopsis* (Brassicaceae) has demonstrated positive correlations between degree of inbreeding and plasticity (Lewis, 1954; Pederson, 1968). Schlichting and Levin (1986) examined the effects of inbreeding on genotype by environment interactions of a self-compatible cultivar, *Phlox drummondii* Hook. (Polemoniaceae). Members of the genus *Phlox* are normally obligately outcrossing. The authors found significant genetic effects (outcrossing and inbreeding lines differed in trait means) and treatment effects. In 75% of the cases inbred and outcrossed lines responded similarly to treatments (similarity in plasticity); conversely, 25% of the traits responded differentially to inbreeding levels (significant variation in plasticity). Overall there was no correlation between increased inbreeding and greater expression of phenotypic plasticity. However, in order to draw inferences to natural settings, as this work was completed on a *Phlox* cultivar, additional studies of native species are required. These three published studies together suggest that the interaction between inbreeding and plasticity is a crucial ecological-genetic interaction that warrants further empirical investigation.

A logical extension of the above studies in a conservation framework is to compare taxa or populations that vary naturally in their levels of inbreeding and habitat heterogeneity and measure phenotypic plasticity of families across environments. For non-native taxa, does a positive correlation between inbreeding and *opportunistic* phenotypic plasticity act as an indicator of potential invasiveness? For restoration projects, selecting native species with: (1) a history of genetic variation for plasticity, (2) possibly *adaptive* phenotypic plasticity across naturally occurring environmental gradients, and (3) a history of inbreeding may be the most appropriate approaches to ensure success, as their chances of establishment may be greatest.

Summary

Some of the more pressing issues in conservation biology center around: (1) predicting the fate of small, isolated populations (e.g., Menges, 1998), (2) ensuring the successful reintroduction of endangered species back into natural habitats, and (3) understanding the establishment of species beyond their native ranges (Chornesky & Randall, 2003; Denslow, 2003). In this paper we recognize important similarities in the genetic and ecological challenges that face each of these types of populations. In all three cases small population sizes will necessarily lead to increased levels of inbreeding and the likely expression of inbreeding depression. The ability of these populations to persist will depend, in part, on the magnitude of inbreeding depression, variation in the response of families to inbreeding, and the ability of selection to remove (or purge) the genetic load that causes inbreeding depression. These, in turn, will depend on the genetic basis of inbreeding depression (overdominance or dominance, epistasis, and the number of loci involved) and the historic mating system of the species. The loss of genetic variation caused by inbreeding and drift in these small populations will restrict their evolutionary potential, placing a high premium on the ability of plants to respond plastically to environmental variation. The ability of plants to make appropriate phenotypic adjustments in truly novel environments, an ability we refer to as *opportunistic plasticity,* may be particularly critical in the case of introductions in ecological restoration work where habitats resemble, but may not be identical to, seed collection sites or in the establishment of exotic species in non-native locations where habitats may differ dramatically from native sites. Whenever plants are not growing in their native environment, they have by default not had the opportunity to adapt specifically to this new environment. Although plasticity may be an important means of dealing with environmental heterogeneity in small populations, unfortunately we have almost no data on the interaction between inbreeding and plasticity in plants. The science and practice of conservation biology has generally appreciated the importance of inbreeding, but we feel that it will benefit greatly by consideration of its potential interactions with plasticity and their role in the establishment phase of small populations. The uniquely rich literature on inbreeding and plasticity in *Mimulus guttatus* make this plant an attrac-

tive model system for studying how these issues act separately and in concert in small, inbreeding populations.

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LOSS OF GENETIC DIVERSITY AND ERRONEOUS PHYLOGEOGRAPHICAL INFERENCES IN *LITHOCARPUS KONISHII* (FAGACEAE) OF TAIWAN CAUSED BY THE CHI-CHI EARTHQUAKE: IMPLICATIONS FOR CONSERVATION[1]

Kuo-Hsiang Hung,[2,5] *Tsai-Wen Hsu,*[3,5] *Barbara A. Schaal,*[4] *and Tzen-Yuh Chiang*[2,6]

Abstract

The effect of natural catastrophic events, such as volcanic eruptions and earthquakes, on the genetic structure of species has been infrequently studied. The 1999 Chi-Chi Earthquake of Taiwan resulted in population extinction of *Lithocarpus konishii* (Fagaceae), an endangered species, and provides a case study for assessing impacts of natural catastrophes on genetic diversity. Genetic diversity of the *atp*B-*rbc*L intergenic spacer of cpDNA and the intron 2 of NADH dehydrogenase subunit 7 gene of mtDNA in *L. konishii* was determined before and after the earthquake. Loss of rare polymorphisms due to extinction of an entire population at the earthquake epicenter contributed to the reduction of genetic diversity within species in both cpDNA and mtDNA. Star-like phylogenies and significantly negative Tajima's D statistics suggest a history of recent expansion of the species, which, however, is not confirmed by a nested clade analysis. Phylogeographical inferences were made before and after the earthquake; differences in the phylogeographic analysis suggest that long-range dispersal inferences may be misidentified due to loss of haplotypes and clades in geographical regions of population extinction. Tests of genetic and ecological exchangeability indicate that *Lithocarpus* populations should be recognized as different conservation units that should be managed separately.

Key words: Chi-Chi Earthquake, cpDNA, genetic diversity, *Lithocarpus konishii*, minimum spanning network, mtDNA, NCA, phylogeography.

Population genetic studies over the last decade have revealed that many plant or animal species can be structured into phylogenetic units that often correspond to geographical regions associated with vicariance and glaciation (e.g., Avise et al., 1987; Avise, 1992; Riddle, 1995; Manos et al., 1999). Phylogeographical patterns of many taxa that evolved through glacial cycles or vicariance events have been well demonstrated based on genealogical information of organelle DNAs, e.g., *Pinus* (Latta & Mitton, 1997), *Abies* (Tsumura & Suyama, 1998), *Cycas* (Huang et al., 2001), *Fagus* (Demesure et al., 1996), *Quercus* (Petit et al., 1997), *Alnus* (King & Ferris, 1998), *Kandelia* (T. Y. Chiang et al., 2001), and *Beta* (Desplanque et al., 2000). In addition to the vicariance and glaciation cycles, fire is also one of the natural disturbances in boreal forests, with a major impact on forest structure and dynamics (Moore, 1996). Until recently, fires reoccurred in boreal forests once to twice per century, annually affecting about 1% of the landscape (Esseen et al., 1997); forest fires shaped the population structure and fates of species (cf. Parker et al., 2001; Johannesson et al., 2001). Like forest fires, earthquakes have the potential to change geographical structure and alter habitats, leading to fluctu-

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[2] Department of Life Science, Cheng-Kung University, Tainan, Taiwan 701.

[3] Taiwan Endemic Species Research Institute, Nantou, Taiwan 521.

[4] Department of Biology, Washington University, St. Louis, Missouri 63130, U.S.A.

[5] Authors contributed to this work equally.

[6] Corresponding author, tychiang@mail.ncku.edu.tw.

ations in genetic diversity and population structure of species within a short time span. Nevertheless, to date, few studies have assessed the influences of such catastrophes on genetic diversity in natural populations.

On 21 September 1999, a devastating earthquake (7.5 on the Richter scale) with three large aftershocks (6.2–6.4) occurred at Chi-Chi in central Taiwan and caused extensive casualties and damage to an extent not experienced in the recent history of Taiwan (Kao & Chen, 2000). This earthquake is referred to as the 921 Earthquake or Chi-Chi Earthquake. The island of Taiwan is at the boundary of the Eurasian and Philippine tectonic plates and is a constituent of the island-arc system along the western edge of the Pacific Ocean. Geologically, Taiwan connects the Ryukyu Island-arc to the north and the Philippine Island-arc to the south (Vita-Finzi, 2000). Along the island-arcs in East Asia, earthquakes occur frequently due to unstable geotectonic structures. As is typical of large earthquakes in steep mountainous regions, well over 1000 landslides were recorded in the region affected by strong ground movement. Landslides on Mt. Juofenger at the earthquake epicenter denuded large regions of vegetation and caused local extinction of many species, including an endemic species of Taiwan, *Lithocarpus konishii* (Hayata) Hayata (Fagaceae).

Lithocarpus konishii, a dominant species of broadleaf forests, grows at low elevations in central and southern Taiwan (Liu & Liao, 1976). *Lithocarpus* trees are 4–9 m in height. Leaves are oblong to obovate with revolute margins and obtuse apices; fruits are rounded nuts in cupules with tomentose scales. Many lowland broadleaf forests with their constituent species have been lost due to human activities (T. Y. Chiang et al., 2004). Like many other lauraceous and fagaceous plants of the island, the number and size of *L. konishii* populations have dramatically decreased. Based on previous collection records (Liao, 1996) and herbarium specimens, many populations of *L. konishii* have disappeared from the wild, especially those of East Taiwan. This oak species is now restricted to sporadic populations on governmental and public lands. *Lithocarpus konishii* has low economic value as a wood source; no human cultivation has been recorded.

In general, plant populations in central and southeastern Taiwan have the highest levels of genetic heterozygosity on the island (Lin, 2001). Lin (2001) found that *Michelia formosana* Masam. & Suzuki populations of central Taiwan harbor more genetic polymorphisms than populations in other regions. Huang et al. (2002) identified glacial refugia for *Fagus* in central Taiwan based on mtDNA, indicating possible hot spots in central Taiwan for the conservation of genetic diversity. The landscape destruction of the Chi-Chi Earthquake in the center of Taiwan could have substantial impact on both the survival of many plant populations and also on the genetic diversity maintained within those populations.

Molecular markers of organelle DNA with low rates of recombination are useful for resolving phylogeographical patterns, population structure, and genetic diversity and assessing the range expansion and migration of species (Avise, 1994; Ouborg et al., 1999; Ennos, 2001; Provan et al., 2001). In plants, chloroplast DNA in general tends to evolve slowly, but recently moderate to high levels of genetic variation have been detected between closely related species and between populations (Ohsako & Ohnishi, 2000). Because one or both organelle genomes are often maternally inherited in plants (Birky, 1995; Mogensen, 1996), with occasional paternal leakage, organelle genomes are particularly well suited for investigating processes associated with dispersal and range expansions (Cruzan & Templeton, 2000; Petit et al., 2001) and the contribution of seed movement to total gene flow (McCauley, 1994, 1995; Cain et al., 2000; Orive & Asmussen, 2000). As in most plants, organelle DNAs in oaks is maternally inherited, and it allows a direct study of seed-mediated dispersal and gene flow and is consequently particularly useful to infer recolonization routes (Rebound & Zeyl, 1993; Dumolin et al., 1995; Lumaret et al., 2002; T. Y. Chiang et al., 2004). Seed dispersal in *Lithocarpus konishii* is mediated by foraging of rodents, e.g., squirrels (Hung et al., in press). Ecological observations found that most migration of the seed carriers is restricted to within populations, given the substantial geographical barriers of mountains and human-dominated landscapes that exist between forest remnants (Hung et al., in press). Because gene flow (both seed and pollen) is restricted, we expect *L. konishii* to have an isolation-by-distance population structure.

In the current study, five relict populations of *Lithocarpus konishii* were sampled from central and southern Taiwan. During the course of botanical inventory, one population on Juofenger Mountain was sampled one week before the Chi-Chi Earthquake. We used the *atp*B-*rbc*L intergenic spacer of cpDNA and intron 2 of the NADH dehydrogenase subunit 7 gene of mtDNA as molecular markers to examine the impact of the Chi-Chi Earthquake on genetic diversity and population structure of *L. konishii*. The phylogeographical structure of genetic varia-

tion among populations of *L. konishii* was determined before and after the earthquake.

Materials and Methods

POPULATION SAMPLES

Due to recent human over-exploitation, many previously recorded populations, such as those of eastern Taiwan (Liao, 1996), have gone extinct from the wild. Five extant populations (117 individuals) of *Lithocarpus konishii,* which are 5 to 260 km apart, were sampled (Table 1, Fig. 1). The KB population at the Mt. Juofenger was sampled before the Chi-Chi Earthquake. Young leaves were collected in the field and dried with silica gel.

DNA EXTRACTION, PCR, AND SEQUENCING

Leaf tissue was ground to powder in liquid nitrogen and stored at −70°C. Genomic DNA was extracted from leaf tissue following a CTAB procedure (Murray & Thompson, 1980). The *atp*B-*rbc*L noncoding spacer of cpDNA and intron 2 of the NADH dehydrogenase subunit 7 gene of mtDNA were amplified and sequenced. PCR amplification was carried out in 100 μL reaction using 10 ng of template DNA, 10 μL of 10X reaction buffer, 10 μL $MgCl_2$ (25 mM), 10 μL dNTP mix (8 mM), 10 pmole of each primer, 10 μL of 10% NP-40, and 2 U of *Taq* polymerase (Promega, Madison, U.S.A.). The reaction was programmed on an MJ Thermal Cycler (PTC 100) as one cycle of denaturation at 95°C for 4 min., 30 cycles denaturation at 92°C for 45 sec., annealing at 52°C for 1 min. 15 sec., and extension at 72°C for 1 min. 30 sec., followed by another extension at 72°C for 10 min. A pair of universal primers for cpDNA *atp*B-*rbc*L spacer (T. Y. Chiang et al., 1998) or the intron 2 of NADH dehydrogenase subunit 7 gene (Demesure et al., 1995), dNTP, and *Taq* polymerase were added to the above ice-cold mix. Reaction was restarted at the first annealing at 52°C.

PCR products were purified by electrophoresis in 1.0% agarose gel using 1 X TAE buffer. The gel was stained with ethidium bromide and the desired DNA band was cut and eluted using agarose gel purification (QIAGEN). Purified DNA was ligated to a pGEM-T easy vector (Promega). Five clones of the plasmid DNA were selected randomly and purified using a plasmid mini kit (QIAGEN). Purified plasmid DNAs were sequenced in both directions by standard methods using the *Taq* dye deoxy terminator cycle sequencing kit (Perkin Elmer) on an Applied Biosystems Model 377A automated sequencer (Applied Biosystems). Primers for se-

Table 1. Populations of *Lithocarpus konishii* samples for DNA sequencing. The number of individuals sampled and sequenced is indicated. Nucleotide diversity (π), haplotype numbers, and haplotype diversity (*h*) are indicated.

Locations	Coordinate	Symbol	Sample size	Nucleotide diversity (π) (%)		Haplotype numbers		Haplotype diversity (*h*)	
				cpDNA	mtDNA	cpDNA	mtDNA	cpDNA	mtDNA
Overall			117	2.469 ± 0.793	0.160 ± 0.099	24	27	0.697	0.666
Overall (excluding KB)			100	2.153 ± 0.752	0.144 ± 0.087	16	17	0.689	0.608
Sun Moon Lake	23°50′N. 120°55′E	KA	12	0.101 ± 0.076	0.127 ± 0.080	4	3	0.682	0.318
Mt. Juofenger	23°56′N. 120°50′E	KB	17	4.335 ± 1.660	0.259 ± 0.174	10	11	0.794	0.904
Carp Lake	24°21′N. 120°48′E	KC	44	1.935 ± 0.973	0.252 ± 0.157	7	9	0.462	0.759
Tahan Forest Road	22°24′N. 120°38′E	CD	12	6.877 ± 1.698	0.073 ± 0.038	3	3	0.621	0.727
Chingshuiying	22°25′N. 120°45′E	CE	32	0.141 ± 0.065	0.053 ± 0.042	5	5	0.708	0.601

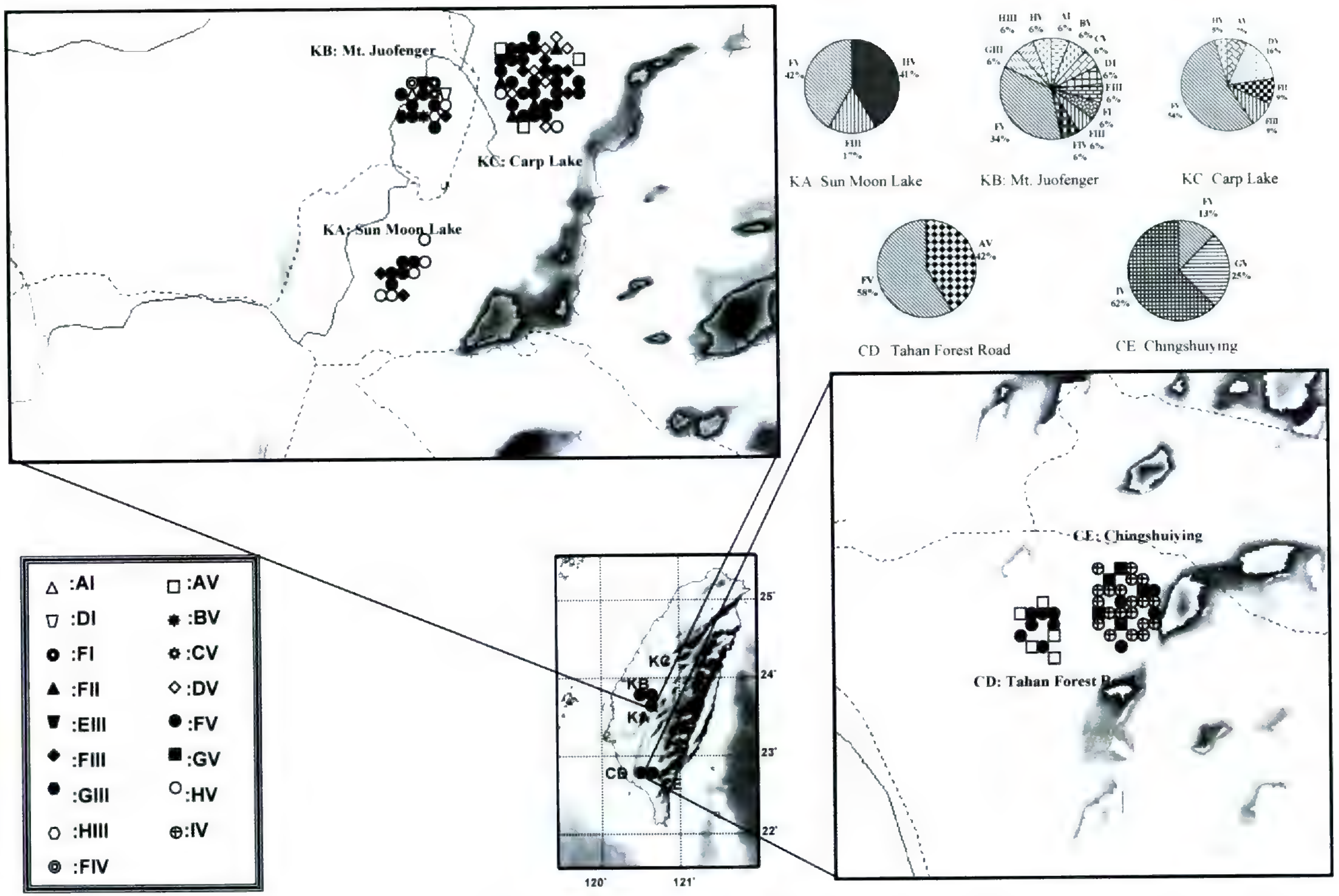

Figure 1. Map showing the spatial distribution and genetic composition (chlorotype-mitotype associations) of populations of *Lithocarpus konishii*. KA: Sun Moon Lake, KB: Mt. Juofenger, KC: Carp Lake, CD: Tahan Forest Road, CE: Chingshuiying.

quence determination were T7-promoter and SP6-promoter located on the p-GEM-T easy Vector termination site.

SEQUENCE ALIGNMENT AND PHYLOGENETIC ANALYSIS

Nucleotide sequences were aligned with the program CLUSTAL V (Higgins et al., 1992) and later adjusted manually. Neighbor-joining (NJ) analysis was performed with the software MEGA (Kumar et al., 1993) by calculating Kimura's (1980) two-parameter distance and excluding the gaps. Confidence of the resulting tree was tested by bootstrapping (Felsenstein, 1985) with 1000 replicates using unweighted characters. The number of mutations between haplotypes in pairwise comparisons, calculated using MEGA (Kumar et al., 1993), was used to construct a minimum spanning network with the aid of the MINSPNET (Excoffier & Smouse, 1994). After linking haplotypes into a clade, closely related clades were linked further to form a higher-level group via hierarchical linking, and a nested network was generated (cf. T. Y. Chiang & Schaal, 1999). In this study, the use of the term "clade" follows Templeton et al. (1995).

Levels of inter- and intra-population genetic diversity were quantified by indices of haplotype diversity (h) (Nei & Tajima, 1983) and pairwise estimates of nucleotide divergence (π) (Jukes & Cantor, 1969) using DnaSP (Vers. 3.0, Rozas & Rozas, 1999). Patterns of geographical subdivision and gene flow were also estimated hierarchically with the aid of DnaSP. A measure of gene flow within and among regions (populations), F_{st}, was obtained from Nm, the number of female migrants per generation between populations. It was estimated using the equation $F_{st} = 1/(1 + 2Nm)$, where N is the female effective population size and m is the female migration rate (Slatkin, 1993).

Geographical associations of haplotypes and clades within the minimum spanning network were tested by using program GeoDis (Posada et al., 2000). Two major statistics were calculated: the clade distance (Dc), a value of the geographical spread of a clade, and the nested clade distance (Dn), a value of the geographical distribution of a clade relative to other clades in the higher-level nesting category. These measures of geographical distribution were used to infer the historical processes following the key of Templeton et al. (1995) and Templeton (2004).

RESULTS

The sequence length of *atp*B-*rbc*L intergenic spacer of cpDNA varied from 809 to 871 bp. In total, 902 bp of the consensus length was aligned. The intron 2 region of the NADH dehydrogenase subunit 7 gene of mtDNA in *Lithocarpus konishii* was also amplified and sequenced, with a length varying from 1327 to 1337 bp and a consensus length of 1369 bp. In total, 24 and 27 haplotypes were detected in cpDNA and mtDNA, respectively.

The KB population from the earthquake epicenter in central Taiwan had the highest haplotype number in both organelle genes, namely 10 for cpDNA and 11 for mtDNA (Table 1). As expected, haplotype and nucleotide diversity of cpDNA (h = 0.697, π = 0.02469) were higher than those of mtDNA (h = 0.666, π = 0.00160) in *L. konishii*. The highest levels of haplotype and nucleotide diversities of cp- and mt-DNAs were detected in the KB population (Table 1). Compared to the genetic composition of populations of *L. konishii* before the earthquake, eight cpDNA haplotypes and ten mtDNA haplotypes disappeared from the wild due to the extinction of population KB at the epicenter. After the Chi-Chi Earthquake, levels of haplotype and nucleotide diversities declined more in cpDNA (h = 0.697 vs. 0.689, π = 0.02469 vs. 0.02153) than in mtDNA (h = 0.666 vs. 0.608, π = 0.00160 vs. 0.00144) (Table 1).

In order to address the relationships of haplotypes in *Lithocarpus konishii*, a minimum spanning network was recovered based on the mutational changes between haplotypes (Fig. 2). The chloroplast DNA sequences of *L. konishii* are distinct from those of *L. formosanus* (Skan) Hayata and *L. dodonaeifolius* (Hayata) Hayata (T. Y. Chiang et al., 2004) with more than 108 nucleotide sites different. In contrast, all populations are polymorphic for cpDNA. Two major clades, separated by 101 mutations, and nine clades were identified: clade 3–1 consisting of clades A, B, and C, and clade 3–2 consisting of clades D–I. Clade F is abundant among the nine clades, with an overall frequency of 50.6% (Table 2). Geographically, clades B, C, and E were found only in the KB population and were lost from the species after the earthquake, while clade I was only present in the CE population (Table 2; Fig. 2). The extinct KB population contained haplotypes from all clades, except for clade I (Table 2).

A spanning network was reconstructed based on the variation of intron 2 of NADH dehydrogenase subunit 7 gene of mtDNA (Fig. 3). As for cpDNA, populations of *Lithocarpus konishii* were polymorphic for mtDNA, except for CD and CE populations. Five major clades, I–V, were identified. Haplotpes from clade V (84.5%) were most frequent and were widely distributed in all populations of *L.*

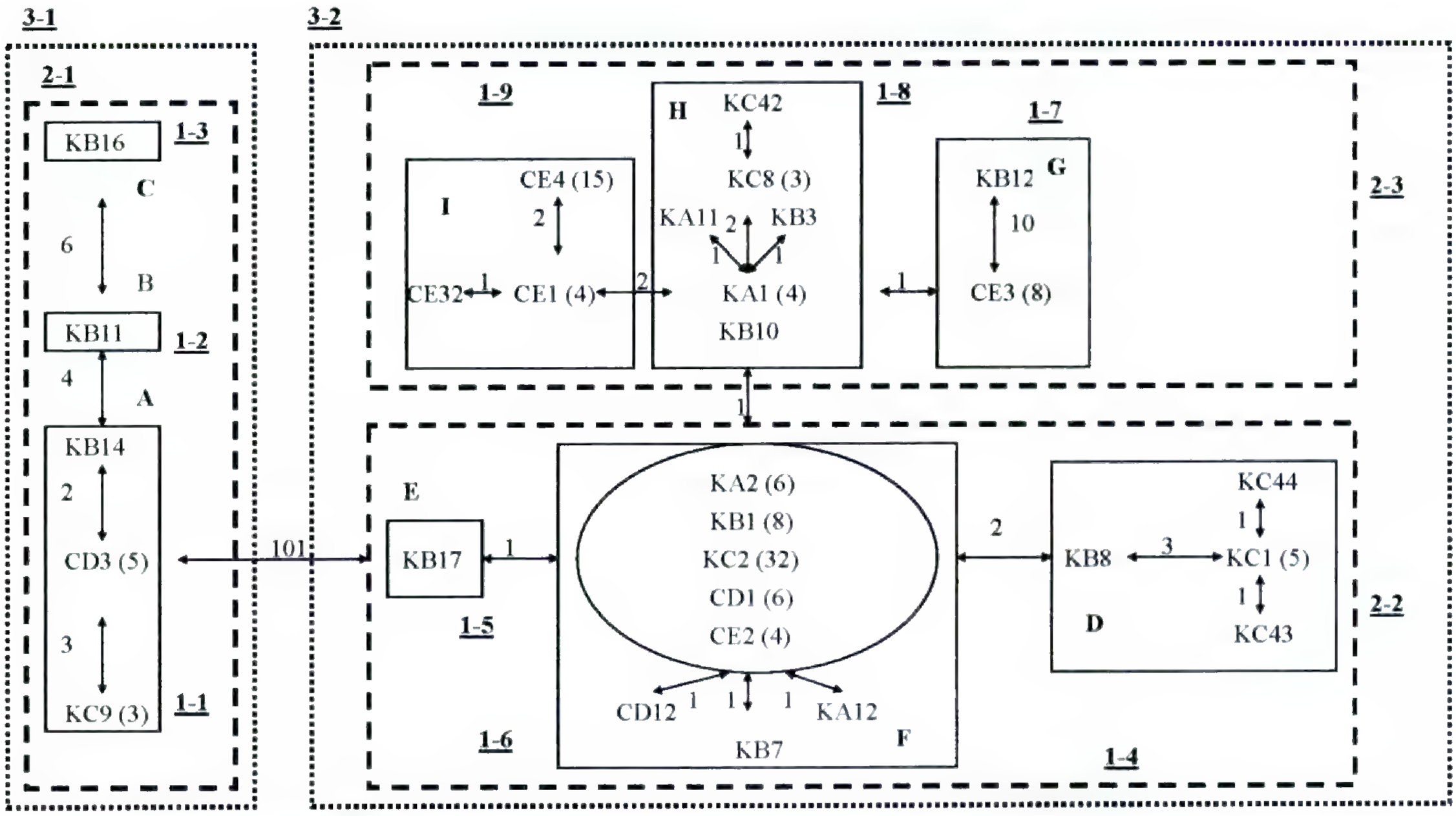

Figure 2. Minimum spanning network of *Lithocarpus konishii* based on the mutational changes between sequences of cpDNA. Clades A to I, and replicate number of each haplotype are indicated.

konishii (Table 2); while clades I and IV were found only in the KB population and became extinct after the earthquake.

For resolving the phylogeographical ambiguities, a nested clade analysis was conducted based on the hierarchical relationships between haplotypes and between clades in the networks. A significant geographical pattern was detected at 2-step and 3-step clade levels in the cpDNA data. Two clades at network tips, clades 1-3 and 1-9, were restricted to unique geographical regions, while interior clades 1-1, 1-6, and 1-8 were widespread. Values of the clade distance (Dc), an estimate of the geographical spread of a clade, and the nested clade distance (Dn), an estimate of the geographical distribution of a clade relative to other clades in the higher-level nesting category, for each clade were determined from the geographical distribution of haplotypes. These values were then used to interpret historical and ongoing processes following the key of Templeton et al. (1995) (Table 3). Restricted seed movement with isolation by distance was identified in clades 1-6, 1-8, 2-2, 2-3, and 3-1, while restricted gene flow coupled with occasional long-distance dispersal contributed to the spatial distribution of haplotypes in clades 1-1 and 3-2. Interestingly, after removing the extinct KB population from the nested clade analysis, phylogeographical patterns became undetectable in clades 1-1, 1-6, and 2-2, and restricted gene flow with long-distance dispersal was identified as the phylogeographical pattern for clade 3-1 (Table 3).

Based on mtDNA data, restricted gene flow with isolation by distance was indicated as a major pattern in clades 2-1 and 3-2, while restricted gene flow coupled with occasional between-population dispersal was identified as a force shaping clade 1-5. No conclusive patterns can be determined for the total cladogram (Table 4). For the cladogram without the KB population, a phylogeographical

Table 2. Distributions and frequencies of cp- and mt-clades in *L. konishii*.

DNA	KA	KB	KC	CD	CE	Total
cpDNA-clade						
A		1	3	5		9 (7.6%)
B		1				1 (0.9%)
C		1				1 (0.9%)
D		1	7			8 (6.7%)
E		1				1 (0.9%)
F	7	9	32	7	4	59 (50.6%)
G		1			8	9 (7.6%)
H	5	2	2			9 (7.6%)
I					20	20 (17.2%)
mtDNA-clade						
I		3				3 (2.7%)
II			4			4 (3.3%)
III	2	4	4			10 (8.6%)
IV		1				1 (0.9%)
V	10	9	36	12	32	99 (84.5%)
Total	12	17	44	12	32	117 (100%)

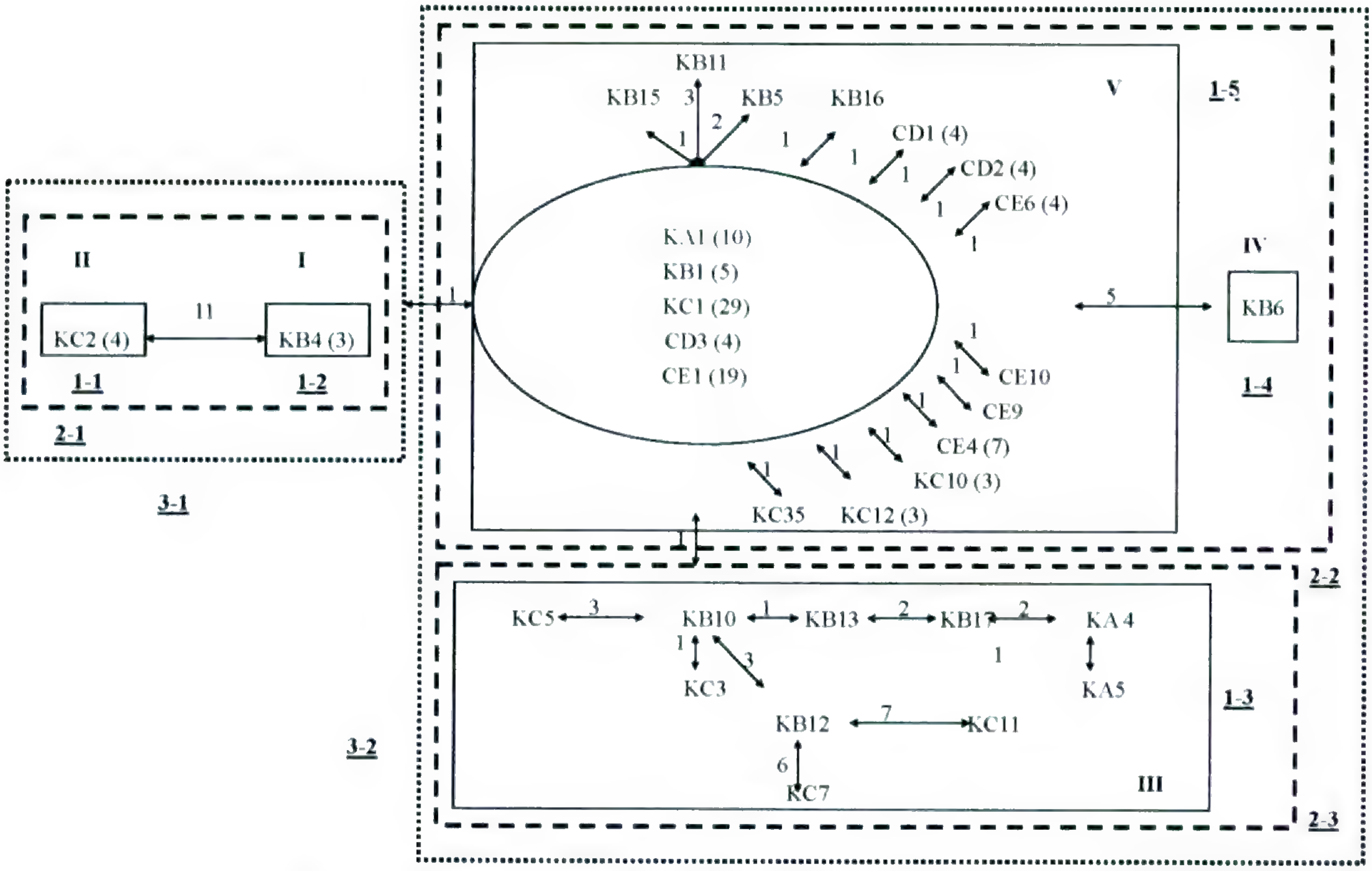

Figure 3. Minimum spanning network of *Lithocarpus konishii* based on the mutational changes between sequences of mtDNA. Clades I to V, and replicate number of each haplotype are indicated.

pattern of occasional long-distance dispersal was identified in clade 2-1.

Low to medium levels of genetic differentiation at the cpDNA intergenic spacer were detected among populations of *Lithocarpus konishii*. Pairwise comparisons revealed that most *Nm* values deduced from the cpDNA sequence are greater than 1, with a range from 0.84 (between KA and CE) to 73.90 (between KB and KC). Likewise, mtDNA sequences revealed no geographical structuring, as indicated by high *Nm* values (1.77 to 58.65) and low to medium F_{st} values (0.22020 to 0.07292) between populations (Table 5). High *Nm* values deduced from both organelle sequences might reflect frequent gene flow between oak populations.

Discussion

Historical and current migration in *Lithocarpus konishii*

In this study, we investigated the genetic diversity of cp- and mtDNAs and population genetic structure in *Lithocarpus konishii*. As expected, this oak species possessed higher levels of nucleotide diversity in cpDNA than in mtDNA due to the differences in the overall rate of nucleotide substitutions for the two genomes (cf. Li, 1997). Nucleotide diversity of cpDNA of the endangered *L. konishii* was relatively high compared to other plants, e.g., California pine (π = 0.003) (Hong et al., 1993), *Michelia formosana* (π = 0.01063) (Lu et al., 2002), *Cunninghamia konishii* Hayata (π = 0.01018) (Lu et al., 2001), *Cycas taitungensis* C. F. Shen et al. (π = 0.01268) (Huang et al., 2001), *Dunnia sinensis* Tutcher (π = 0.0022) (Ge et al., 2002), and *Lithocarpus formosanus* (π = 0.081) (T. Y. Chiang et al., 2004). Relative to most angiosperms, the nucleotide diversity of mtDNA of *L. konishii* was also high, although still lower than that of *Cycas taitungensis* (π = 0.02637) (Huang et al., 2001) and *Dunnia sinensis* (π = 0.0019) (Ge et al., 2002). It has been known that endangered or threatened species tend to have depauperate genetic variability due to small population size (O'Brien, 1994; Taylor et al., 1994; Vrijenhoek, 1994; Mundy et al., 1997; Gibbs et al., 1998). Such unusually high levels of genetic diversity in *L. konishii* reflect that this endangered endemic species must have been shaped by other evolutionary forces in addition to random genetic drift. Populations may have residual levels of genetic variation before extirpation.

Although high *Nm* values were deduced from both organelle DNAs, they are unlikely to represent current gene flow among populations due to constraints of seed dispersal across the geographical range of the species (T. Y. Chiang et al., 2004;

Table 3. Nested contingency analysis of geographical associations and phylogeographical inferences made from a nested haplotype analysis of *L. konishii* based on chloroplast DNA.

	Clade	Permutational chi-square statistic	Probability	Clade key	Inferences
Both extant and extinct populations	Clade 1-1	18.0000	0.0030	1, 2, 3, 5, 6, 7, YES	restricted gene flow/dispersal but with some long-distance dispersal
	Clade 1-6	12.9218	0.2550	1, 2, 11, 17, 4, NO	restricted gene flow with isolation by distance
	Clade 1-8	15.8400	0.0140	1, 2, 3, 4, NO	restricted gene flow with isolation by distance
	Clade 2-2	6.5185	0.1100	1, 2, 3, 4, NO	restricted gene flow with isolation by distance
	Clade 2-3	9.1283	0.4000	1, 2, 3, 4, NO	restricted gene flow with isolation by distance
	Clade 3-1	35.3862	0.0000	1, 2, 3, 4, NO	restricted gene flow with isolation by distance
	Clade 3-2	59.5765	0.0000	1, 2, 3, 5, 6, 7, YES	restricted gene flow/dispersal but with some long-distance dispersal
	Total cladogram	20.9339	0.0010	1	non-significant
Extant populations	Clade 1-8	9.0000	0.0280	1, 2, 3, 4, NO	restricted gene flow with isolation by distance
	Clade 2-3	35.0000	0.0000	1, 2, 3, 4, NO	restricted gene flow with isolation by distance
	Clade 3-1	8.0000	0.0180	1, 2, 3, 5, 6, 7, YES	restricted gene flow/dispersal but with some long-distance dispersal
	Clade 3-2	56.7053	0.0000	1, 2, 3, 5, 6, 7, YES	restricted gene flow/dispersal but with some long-distance dispersal
	Total cladogram	22.3897	0.0010	1	non-signficant

Hung et al., in press). *Nm* values may also be a reflection of ancestral polymorphisms or may be the result of gene flow among populations when populations were more contiguously distributed. However, the phylogeographical pattern in *Lithocarpus konishii* does not conform to an "isolation by distance" model (i.e., the correlation between degree of genetic differentiation and geographical distance), which could indicate long-distance gene dispersal in the past. In this study, a smaller genetic distance frequently existed between two geographically distant populations than between sequences within the same population, e.g., haplotypes of KB1 and KC12 (= KC33, KC34) separated by a single mutation versus KB1 and KB6 with 5 mutations in mtDNA. Such patchy distributions (Fig. 1) of closely related organelle haplotypes among populations have also been observed in many European tree species that survived glacial periods (Ferris et al., 1995; Petit et al., 1997; King & Ferris, 1998), as well as in *Cunninghamia konishii* (Lu et al., 2001), *Michelia formosana* (Lu et al., 2002), and *Lithocarpus formosanus* (T. Y. Chiang et al., 2004) of Taiwan. According to geological record, since the late Pleistocene, Taiwan was the southeastern edge of the Asian continent before the formation of Taiwan Strait about 100,000 years BP (Lin, 1966; Tsukada, 1966; Kizaki & Oshiro, 1977). This continental island was linked to the mainland via a land bridge and was not completely isolated until the last glacier retreated ca. 18,000 to 20,000 years BP (Lin, 1966). Geological evidence indicates that ice ages have occurred at regular intervals of approximately 100,000 years followed by warm periods of about 20,000 years (Milankovitch cycles) (cf. Bennett, 1990; King & Ferris, 1998). During the glacial maximum, many oaks and conifers previously dominant in the northern part of eastern Asia were forced to migrate into refugia in southern China and Taiwan (T. Y. Chiang et al., 1999), which were mostly distributed at low elevations (cf. Tsukada, 1966). During the subse-

Table 4. Nested contingency analysis of geographical associations and phylogeographical inferences made from a nested haplotype analysis of *L. konishii* based on mitochondrial DNA.

	Clade	Permutational chi-square statistics	Probability	Clade key	Inferences
Both extant and extinct populations	Clade 1-5	142.5075	0.0000	1, 2, 3, 5, 6, 7, YES	restricted gene flow/dispersal but with some long-distance dispersal
	Clade 2-1	7.0000	0.0280	1, 2, 3, 4, NO	restricted gene flow with isolation by distance
	Clade 3-2	11.7019	0.018	1, 2, 3, 4, NO	restricted gene flow with isolation by distance
	Total cladogram	8.4311	0.0740	1, 2	inconclusive outcome
Extant populations	Clade 1-3	19.0000	1.0000	1, 2, 11, 17, NO	inconclusive outcome
	Clade 1-5	142.5075	0.0000	1, 2, 3, 5, 6, 7, YES	restricted gene flow/dispersal but with some long-distance dispersal
	Clade 2-1	7.0000	0.0370	1, 2, 3, 5, 6, 7, YES	restricted gene flow/dispersal but with some long-distance dispersal
	Clade 3-2	11.7019	0.0140	1, 2, 3, 4, NO	restricted gene flow with isolation by distance
	Total cladogram	8.4311	0.0780	1, 2	inconclusive

quent deglaciation, elevated global temperatures forced the lowland plants to migrate to high elevations or local peaks.

Heterogeneous composition of organelle DNAs within populations and low levels of genetic differentiation among populations suggest a likely migrant-pool model (Wade & McCauley, 1990), which describes a dispersal pattern where colonists are recruited from a random sample of all the other populations. Under this model, the number of colonists is likely to be large during recolonization and many ancestral polymorphisms are maintained within populations. In this study, the low level of genetic differentiation among *Lithocarpus konishii* populations suggests that the period of 18,000 years for isolation may not be ample for coalescence. The star-like shape of both cp- and mtDNA genealogies, with one common haplotype and many recent single mutation derivatives (Figs. 2, 3), is consistent with a recent range expansion as are the negative Tajima's D statistics detected for both sequences (Y. C. Chiang et al., 2004; Rueness et al., 2003).

Table 5. Pairwise F_{st} estimates between populations of *L. konishii* based on cpDNA (above diagonal) and mtDNA (below diagonal).

	KA	KB	KC	CD	CE
KA		0.11444	0.07045	0.36223	0.37397
KB	0.00845		0.00672	0.06248	0.13482
KC	0.12579	0.03547		0.22144	0.10395
CD	0.16268	0.13479	0.20579		0.36462
CE	0.09841	0.09620	0.07292	0.22020	

LOSS OF GENETIC DIVERSITY IN *LITHOCARPUS KONISHII* DUE TO THE CHI-CHI EARTHQUAKE

The Chi-Chi Earthquake had a profound effect on the genetic structure of *Lithocarpus konishii*. Our molecular genetic analysis revealed that the KB population in central Taiwan, like many other angiosperms in Taiwan (cf. Lin, 2001; Huang et al., 2002), possessed a large number of haplotypes of cpDNA and mtDNA (10 and 11, respectively) and high levels of genetic diversity and represented a hot spot for the conservation of genetic diversity.

The devastating earthquake eliminated from the species eight cpDNA haplotypes (33.3%), including clades B, C, and E, and 10 mtDNA haplotypes (37.0%), including clades I and IV. The Chi-Chi Earthquake had a severe impact on the levels of genetic diversity within the species. Changes of nucleotide diversity of cpDNA are evident before and after the earthquake, $\pi = 0.02469$ versus 0.02153, with 12.8.0% of the genetic diversity eliminated. Compared to cpDNA, a relatively lower percent (10.0%) of genetic diversity of mtDNA has been lost from this species, although in absolute numbers

more haplotypes went extinct in mtDNA. The loss of this central population due to the earthquake increases the risk of extinction for *L. konishii*; the species is now even more narrowly distributed and the loss of the most genetically diverse populations has dramatically decreased the overall levels of diversity.

PHYLOGEOGRAPHY OF *LITHOCARPUS KONISHII*

Minimum spanning networks, based on two organelle loci, were used to trace the geographical associations among alleles (Templeton et al., 1995). As has been extensively documented, climatic changes influence the distribution and evolution of species in a geographical context; fluctuating cycles of glaciation since the late Pleistocene have constrained the migration of many species (Hewitt, 1996, 1999) and strongly affected the distribution of their genetic variation (Caron et al., 2000). In resolving geographical patterns of variation, nested intraspecific gene networks usually provide greater resolution compared to conventional phylogenetic trees (Crandall & Templeton, 1993).

In *Lithocarpus konishii*, as in many other plants in Taiwan, e.g., *Cycas taitungensis* (Huang et al., 2001), *Cunninghamia konishii* (Lu et al., 2001), *Michelia formosana* (Lu et al., 2002), *Lithocarpus formosanus* and *L. dodonaeifolius* (T. Y. Chiang et al., 2004), *Trema dielsiana* Hand.-Mazz. (Y. C. Chiang et al., 2004), and *Miscanthus sinensis* Andersson (Y. C. Chiang et al., 2003), range expansion occurred after the glaciers retreated and the species spread out from their refugium; the inferences of long-distance dispersal and displacement for tip clades is consistent with range expansion (Tables 3, 4). For example, chloroplast clades/haplotypes at the tip nodes, such as clade I and haplotype KC1, which are restricted to population CE and KC (Figs. 2, 3), respectively, may represent some migrants from the putative refugium at KB during range expansion. Evidence of star-like phylogenies of both cp- and mtDNA genealogies, and significantly negative Tajima's D statistics also suggest a scenario of recent population expansion. However, a history of recent demographics was not supported by nested clade analysis (NCA). The shortcoming of NCA in detecting range expansion, which was also illustrated in a recent phylogeographical analysis of an Iberian lizard (Paulo et al., 2002), may be ascribed to the existence of widespread ancestral (interior) haplotypes in the networks, which contrasts with the prediction that ancestral haplotypes are restricted to the ancestral range while descendent (tip) haplotypes are more widespread under population expansion (cf. Templeton, 1998).

In this study, restricted gene flow with occasional long-distance dispersal, identified by phylogeographical analyses, seems to explain why a model of "isolation by distance" is not supported at the scale of overall species. Nevertheless, the discrepancy in phylogeographical inferences within the same clades before and after the Chi-Chi Earthquake implies that the NCA is sensitive to the stochastic extinction of haplotypes and clades. Although long-range seed dispersal has been recognized as one of the major mechanisms for the postglacial recolonization in European oaks (Petit et al., 1997), here we illustrated that some long-range colonization inferences, three out of eight NCA inferences of this study, may have been misidentified due to extinction of haplotypes (clades) in intervening areas, especially those geographically central to other populations (cf. Masta et al., 2003). Simulations by removing peripheral populations from this analysis, in contrast, do not reveal any additional long-range dispersal events (data not shown), indicating different roles of the populations spanning across a geographical range. Apparently, when intermediate populations are removed, historical stepping-stone migration can be erroneously interpreted as long-distance dispersal among distant, extant populations. Overestimated long-range colonization would become more serious and unavoidable, as species experience frequent and recurrent extinction-recolonization.

MANAGEMENT UNITS FOR CONSERVING *LITHOCARPUS KONISHII*

The Chi-Chi Earthquake caused a dramatic loss of genetic diversity in *Lithocarpus konishii* due to extinction of a single population located at the epicenter. The Mt. Juofenger population harbored a large number of genetic polymorphisms, making this endemic species more threatened. Various criteria have been suggested for defining evolutionarily significant units (ESUs) for species of high conservation priority, including reciprocal monophyly (Moritz, 1994), adaptive variation (Ryder, 1986), and reproductive separation (Waples, 1991). Recognizing ESUs as reciprocally monophyletic groups ensures that all evolutionary heritages within a species can be maintained and that populations of different lineages can be managed separately (Crandall et al., 2000). Nevertheless, in contrast to animal mitochondrial genes, of which reciprocal monophyly is a common characteristic due to fast evolutionary rates, plant organelle DNA

genes, especially those unrelated to speciation (cf. Ting et al., 2000), usually display paraphyly between sister species due to ancestral polymorphisms (Chiang, 2000). Examples include European oaks (Petit et al., 1997), *Lithocarpus formosanus* and *L. dodonaeifolius* (T. Y. Chiang et al., 2004), *Cycas taitungensis* and *C. revoluta* Thunb. (unpublished data), *Amorphophallus* (Chiang & Hong, 1999), *Archangiopteris* (T. Y. Chiang et al., 2002), and *Cunninghamia* (Lu et al., 2001). Frequently encountered paraphyly among closely related plant species suggests that such a monophyly-based definition is not widely applicable to plants (Newton et al., 1999; Crandall et al., 2000).

If Moritz's (1994) criterion of reciprocal monophyly is used here, no single population of *Lithocarpus konishii* can be recognized as a conservation unit due to lack of reciprocal monophyly and low levels of genetic differentiation, even though all populations are geographically isolated. According to the rationale, despite the rampant paraphyly in the oak populations, "awaiting attainment of monophyly within species/populations via coalescent processes" is an explicit policy that could be adopted for conserving such a threatened species. As a consequence, many genetic polymorphisms that were maintained during the paraphyletic stages would be randomly lost from *L. konishii* before the species/populations reach monophyly. A simple dichotomy of monophyly and non-monophyly is insufficient for determining conservation units. In *L. konishii* high levels of genetic diversity within populations may lead conservation biologists to conclude a low conservation priority for this restricted, endemic species. The dramatic loss of genetic diversity due to the devastating Chi-Chi Earthquake reveals how fragile a species like *L. konishii*, with limited population number and size, can be. Although molecular data provide sufficient information for reconstructing phylogeographical patterns of *L. konishii*, defining conservation units solely on the basis of information from genetic markers should be avoided (Taylor & Dizon, 1999).

Crandall et al. (2000) developed 16 categories for identifying population distinctiveness and management practices based on rejection of, or failure to reject, genetic and ecological exchangeabilities in both recent and historical time frames. The dichotomy of historical versus recent events can be made based on particular genetic markers. In this study, both cp- and mt-DNAs indicate large *Nm* values, suggesting historical interchanges between populations. At the same time, our ecological observations reject current exchangeability (both genetic and ecological). Altogether these considerations suggest that *Lithocarpus* populations represent different units for conservation (Case 5(a) of Crandall et al., 2000); populations spanning geographical regions should be managed separately. In addition to preserving adaptive diversity and evolutionary processes across the geographical range of a species, specific threats and recent disturbance in each population should be taken into account before genetic diversity is lost.

Taking genetic and demographical data into consideration in defining conservation units, as opposed to reciprocal monophyly, makes Crandall et al.'s (2000) methodologies more thorough and applicable. Nevertheless, overemphasizing the current ecological exchangeability may make one neglect the role of conservation genetics. If recent ecological exchangeability is rejected, populations would be treated as distinct conservation units; if not, an entire group of populations would be recognized as a single unit. Genetic exchangeability, seemingly, plays a minor role in determining the management action. That is, no matter how different the outcomes of testing of genetic exchangeability, they are unable to change the management units recommended by ecological exchangeability. In this study, molecular data provided sufficient information for reconstructing phylogeographical patterns, which in turn are critical for testing historical, genetic exchangeability. We therefore suggest that defining conservation units solely based on ecological measures should be avoided.

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PHYLOGENETICS OF AMARANTHACEAE BASED ON *mat*K/*trn*K SEQUENCE DATA—EVIDENCE FROM PARSIMONY, LIKELIHOOD, AND BAYESIAN ANALYSES[1]

Kai Müller[2] *and Thomas Borsch*[2]

Abstract

Amaranthaceae and Chenopodiaceae together represent the most species-rich monophyletic group in the angiosperm order Caryophyllales. So far, phylogenetic relationships between Amaranthaceae and Chenopodiaceae have remained unclear. Previous morphological and molecular studies have indicated that most of the currently accepted infrafamilial taxa in Amaranthaceae do not reflect natural groups. With the aim to provide a robust phylogenetic framework for analyzing the evolution of pollen and other phenotypic characters within the family, we conducted maximum parsimony, maximum likelihood, and Bayesian analyses using chloroplast *mat*K/*trn*K DNA sequence data. The Amaranthaceae–Chenopodiaceae lineage was resolved as monophyletic, with Achatocarpaceae and Caryophyllaceae being successive sisters. Within the monophyletic Amaranthaceae, a basal grade of *Bosea* L. (Macaronesian islands, Cyprus, Himalaya), followed by *Charpentiera* Gaudich. (endemic to Hawaii and the Australian Ridge) receives high support. Celosieae appear as sister to *Amaranthus* L. + *Chamissoa* Kunth. While Celosieae were supported as natural, most other currently recognized infrafamiliar taxa were revealed to be para- or polyphyletic. Among former Aervinae, an Achyranthoid and an Aervoid clade were newly recovered. *Pseudoplantago* Suess., sharing some morphological features with Amaranthoideae, was found within Gomphrenoideae rather than being in a position linking both subfamilies. The evolution of morphological characters previously used for classification and of some pollen characters was analyzed based on the *mat*K/*trn*K tree. The recently described metareticulate pollen architecture is reconstructed to have evolved once in the ancestor of a highly supported core Gomphrenoid clade that comprises the traditional Gomphrenoideae but excludes *Iresine* P. Browne. In contrast, the complex stellate pore ornamentation was reconstructed as having evolved at least twice in parallel. Unlike other morphological characters discussed in this paper, pollen characters in general represent morphological synapomorphies circumscribing many clades recovered with molecular data. In addition, the present paper provides a brief survey of the taxonomic history and the current state of research on systematics and evolution in Amaranthaceae.

Key words: Amaranthaceae, Caryophyllales, Chenopodiaceae, phylogenetics, pollen evolution.

With approximately 180 genera and 2500 species (Kühn et al., 1993; Townsend, 1993), the two families Amaranthaceae and Chenopodiaceae together represent the most species-rich lineage in the angiosperm order Caryophyllales. The Amaranthaceae are predominantly tropical, whereas Chenopodiaceae have their centers of diversity in dry temperate and warm temperate areas of both hemispheres, where they are often dominant parts of the vegetation. Both families comprise important crops, such as spinach, quinoa, beet, and grain amaranth. Grain amaranths range among the most promising underexploited food and fodder crops, and their seeds have been reported to contain very

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[2] Nees-Institut für Biodiversität der Pflanzen, Rheinische Friedrich-Wilhelms-Universität Bonn, Meckenheimer Allee 170, 53115 Bonn, Germany. kaimueller@uni-bonn.de.

high amounts of protein (Becker et al., 1981; Dey & Mandal, 1993; Nath et al., 1997).

Relationships between Amaranthaceae and Chenopodiaceae

In terms of their morphology, anatomy, as well as phytochemistry, Amaranthaceae and Chenopodiaceae are very similar. Therefore, they have been regarded as closely related since the early 19th century (Brown, 1810; Bentham & Hooker, 1880; Baillon, 1887; Volkens, 1893; Ulbrich, 1934; Aellen, 1965–1968; Behnke, 1976; Thorne, 1976; Carolin, 1983; Kühn et al., 1993; Townsend, 1993). In spite of problems in identifying distinguishing characters, the majority of authors have treated both families separately, although *Polycnemum* L. and its relatives (*Hemichroa* R. Br., *Nitrophila* S. Watson) have been treated variably, either as belonging to Amaranthaceae (Endlicher, 1837; Moquin-Tandon, 1849; Scott, 1977a) or Chenopodiaceae (most other authors). Polycnemoideae share petaloid tepals, basally united filaments that form a tube, and bilocular anthers with Amaranthaceae, while they are more similar to the remaining Chenopodiaceae in most other respects.

A merger of Chenopodiaceae and Amaranthaceae into one family was advocated only rarely (Baillon, 1887; Malligson, 1922, on the basis of serological studies). However, recently this has been proposed again using the earlier name Amaranthaceae (APG, 1998, 2003). Nevertheless, most of the floristic literature and the immense number of ecological studies still refer to separate Amaranthaceae and Chenopodiaceae (e.g., Gauquelin et al., 1998; Blunden et al., 1999; Deil, 2000), whereas usage of the single-family name Amaranthaceae is rarely found (e.g., Barderas et al., 2002).

So far, only few molecular studies included more than two taxa of Amaranthaceae and Chenopodiaceae in their sampling, and in these, both families were either resolved as sister families (Giannasi et al., 1992; Rettig et al., 1992; Downie & Palmer, 1994; Cuénoud et al., 2002), or Amaranthaceae were identified as nested within Chenopodiaceae (Manhart & Rettig, 1994; Downie et al., 1997; Cuénoud et al., 2002), making Chenopodiaceae paraphyletic. The combination of *rbc*L and partial *mat*K sequences (Cuénoud et al., 2002) yielded high support for two separate monophyletic lineages (99% and 100% bootstrap for Chenopodiaceae and Amaranthaceae, respectively), but since Cuénoud et al. aimed at resolving relationships among major clades of Caryophyllales, their sampling was rather narrow (a total of five genera for Amaranthaceae and Chenopodiaceae). Cladistic analyses of phenotypic characters were comparably indecisive, supporting the paraphyly of Chenopodiaceae in some cases (Scott, 1977a; Carolin, 1983; Rodman, 1990), while demonstrating the sister group relationship of both families in others (Rodman, 1994).

A recent study using *rbc*L sequences and a sampling particularly dense in Chenopodiaceae (Kadereit et al., 2003) found a polytomy of three groups: (1) Amaranthaceae and Polycnemoideae; (2) Beteae (most of the genera in individual lineages; Chenopodiaceae); (3) the remainder of Chenopodiaceae. However, among these deeper nodes only the one uniting all Chenopodiaceae and Amaranthaceae gained statistical support. Analysis of *ndh*F sequences from the two families (Pratt, 2003) resolved Chenopodiaceae as being paraphyletic to Amaranthaceae, but did not yield support for the relationship between both families, either. Moreover, preliminary studies using DNA sequences of the complete *trn*K intron (including *mat*K) demonstrated that whether Chenopodiaceae were resolved as monophyletic or not varied with the taxon composition of the data set and the inference method employed (Müller & Borsch, 2002). Given these inconsistent results, it appeared that further work would be needed to understand relationships between Amaranthaceae and Chenopodiaceae or make decisions regarding family classifications. In the following study, Chenopodiaceae and Amaranthaceae collectively will be referred to as "Chenopodiaceae–Amaranthaceae alliance" and the name "Amaranthaceae" is used in the strict sense of Schinz (1893, 1934) and Townsend (1993).

Position of the Amaranthaceae–Chenopodiaceae Alliance within the Caryophyllales

With respect to the systematic relationships of the alliance in the Caryophyllales, Illecebraceae (Paronychioideae of Caryophyllaceae) had conventionally been regarded as the closest relative since Bentham and Hooker (1880). However, in recent phylogenetic analyses, Achatocarpaceae unequivocally appear as sister to the Amaranthaceae–Chenopodiaceae alliance, based on molecular evidence (*rbc*L: Manhart & Rettig, 1994, Savolainen et al., 2000a; partial *mat*K sequences: Cuénoud et al., 2002; Hilu et al., 2003), and morphological data (Rodman, 1994).

This Amaranthaceae–Chenopodiaceae–Achatocarpaceae clade (here called "ACA clade") is part of "Caryophyllales I" as defined in Hilu et al.

(2003), which comprise the Centrospermae as conventionally delimited (Cronquist & Thorne, 1994) plus Simmondsiaceae, Rhabododendraceae, and Asteropeiaceae.

Early analyses of *rbc*L (Albert et al., 1992; Giannasi et al., 1992; Rettig et al., 1992; Chase et al., 1993; Manhart & Rettig, 1994; Chase & Albert, 1998), later confirmed by nuclear ribosomal 18S (Soltis et al., 1997), partial *mat*K (Cuénoud et al., 2002; Hilu et al., 2003), and *atp*B sequences (Savolainen et al., 2000a), have indicated a monophyletic group that was classified as "expanded Caryophyllales," comprising the traditional Centrospermae along with Plumbaginaceae, Polygonaceae, Tamaricaceae, Frankeniaceae, and a carnivorous clade with Ancistrocladaceae, Dioncophyllaceae, Droseraceae, and Nepenthaceae.

Presently, the precise relationships of the ACA clade in the order still remain somewhat vague. Multiple gene analyses (Savolainen et al., 2000a; Soltis et al., 2000; Cuénoud et al., 2002) offered good support for an ACA clade plus Caryophyllaceae being sister to a clade termed "higher core Caryophyllales," which comprises Agdestidaceae, Sarcobataceae, Gisekiaceae, Barbeuiaceae, Didieriaceae, Basellaceae, Halophytaceae, Nyctaginaceae, Phytolaccaceae, Aizoaceae, Cactaceae, Portulacaceae, and Molluginaceae. Based on a dense sampling comprising all subfamilies, Caryophyllaceae have also been identified as sister of ACA in a recent *rbc*L study (Kadereit et al., 2003). However, persuasive statistical support for this is still lacking, and as indicated by differing taxon sampling, markers, and/or inference methods, alternatively Caryophyllaceae might be sister to a lineage comprising the ACA clade plus the higher core Caryophyllales (Savolainen et al., 2000a; Cuénoud et al., 2002; Hilu et al., 2003). Therefore, the inclusion of a rather extensive outgroup appears warranted in the present study because detailed knowledge about the sister group of the ACA clade is essential for understanding character evolution within this clade. Reinvestigating the ACA relationships based on complete *trn*K intron sequences and indels more than doubles the number of characters compared to previous studies of partial *mat*K.

Diversity, Classification, and Relationships within Amaranthaceae

The Amaranthaceae are most diverse in the Neotropics, tropical and southern Africa, and Australia (e.g., Townsend, 1993). Among the few genera occurring in temperate regions, the most important and well known is *Amaranthus* (pig weeds). The majority of Amaranthaceae in the Neotropics belongs to the Gomphrenoideae. Centers of diversity of Gomphrenoideae are in Central America and Mexico (e.g., *Iresine*, *Tidestromia* Standl.), in various habitats and altitudes of the Andes, as well as in the Chaco, Caatinga, and Cerrado. The largest genera in the New World are *Gomphrena* L. and *Alternanthera* Forssk., which make up most of the high diversity in the central Andes (Ecuador, Peru, and Bolivia), in the subpuna (Argentina, Bolivia), and Caatinga and Cerrado habitats (Brazil). *Pfaffia* Mart. has radiated in tropical savannas and the Chaco. In southern Africa, genera like *Kyphocarpa* Schinz, *Sericorema* Lopr., *Sericocoma* Fenzl, and *Hermbstaedtia* Rchb. are characteristic and particularly diverse, while *Ptilotus* R. Br. has radiated in Australia. Amaranthaceae include annuals, herbaceous perennials, woody lianas (e.g., *Stilbanthus* Hook. f., *Sericostachys* Gilg & Lopr., *Hebanthe* Mart.), shrubs (*Pleuropetalum* Hook. f.), and trees (e.g., *Charpentiera*, some species of *Iresine*, *Nototrichium* (A. Gray) W. F. Hillebr.), and live in diverse habitats ranging from the seashore (*Blutaparon* Raf.) to the semi-desert (*Arthraerua* Schinz). Inflorescences appear to be basically cymose, but often are reduced to a single flower subtended by one bract and two bracteoles.

According to the currently available data (Amaranthaceae database at the Nees Institute), an estimate of diversity in Amaranthaceae results in 77 genera and approximately 840 species in total. The largest genera by far are *Gomphrena*, *Alternanthera*, and *Ptilotus*. *Gomphrena* probably comprises more than 120 species, with many recently described from South America (Ortuño & Borsch, 2005; Pedersen, 1976; Siqueira, 1982; Pedersen, 1990, 2000) and Australia (Palmer, 1998). *Alternanthera* (Neotropical; pantropical weeds) and *Ptilotus* (Australia) contain around 100 and 80 species, respectively (Townsend, 1993).

The most important of the previous classification systems of Amaranthaceae are summarized in Table 1. The first comprehensive treatment intended as a family monograph (Martius, 1825) recognized 28 genera and was followed by a series of overall family treatments (Endlicher, 1837; Moquin-Tandon, 1849; Schinz, 1893; Standley, 1917; Schinz, 1934; Cavaco, 1962; Townsend, 1993). The most extensive historical Flora treatment is by Seubert (1875) in *Flora brasiliensis*, using a classification into three tribes comparable to Endlicher (1837) and Moquin-Tandon (1849). Kuntze (1891) modified a number of generic concepts but did not present any suprageneric classification. A system mainly based

Table 1. Previous classifications of Amaranthaceae.

Endlicher (1837)	Moquin-Tandon (1849)	Baillon (1888)	Bentham & Hooker (1880)	Schinz (1893)	Schinz (1934)	Cavaco (1962)	Townsend (1993)
Celosieae	Celosieae	Célosiées	Celosieae	Celosieae	Amaranthoideae	Celosioideae	Amaranthoideae
Achyrantheae	Achyrantheae	Amarantées	Amarantheae	Amarantheae	Celosieae		Celosieae
Amarantheae	Amarantheae		Euamarantheae	Amaranthinae	Amarantheae	Amaranthoideae	Amarantheae
Aerveae	Aerveae		Achyranthae	Achyranthinae	Amaranthinae	Amarantheae	Amaranthinae
Desmochaeteae	Desmochaeteae	Gomphrénées	Gomphreneae	Gomphrenoideae	Achyranthinae	Achyranthinae	Aervinae
Polycnemeae	Polycnemeae	Microtérées		Gomphreneae	Gomphrenoideae	Gomphrenoideae	Gomphrenoideae
Gomphreneae	Gomphreneae	Leucastérées		Gomphreninae	Gomphreneae	Gomphreneae	Gomphreneae
	14 sections			Froelichiinae	Gomphreninae	Gomphreninae	Gomphreninae
				Brayulineae	Froelichiinae	Froelichiinae	Froelichiinae
				Brayulineinae	Brayulineae	Tidestromiinae	Tidestromiinae
				Tidestromiinae	Brayulineae	Brayulineae	Pseudoplantageae
				Guillemineae	Tidestromiinae		

on floral morphology and embryology (Cavaco, 1962), distinguishing two additional subfamilies (Brayulineoideae, Celosioideae), remained mostly unaccepted by authors afterward. The presently accepted classification is the one proposed by Townsend (1993), which is largely based upon the work of Schinz (1893, 1934). Schinz himself derived his concept from Bentham and Hooker (1880) and first recognized two subfamilies, the Amaranthoideae (with bilocular = 4-locellate anthers), and the Gomphrenoideae (with unilocular = 2-locellate anthers). Schinz, however, made substantial changes in the latter subfamily by distinguishing the tribes Gomphreneae (with Gomphreninae and Froelichiinae) and Guillemineae (Schinz, 1893). In the second edition of his treatment, he changed Guillemineae to Brayulineae and introduced a new subtribe called Tidestromiinae (Schinz, 1934). The genus *Pseudoplantago,* displaying a mixture of amaranthoid and gomphrenoid floral morphology, was classified in its own tribe (Covas, 1939) soon after its description (Suessenguth, 1934) and was considered intermediate between the two subfamilies (Eliasson, 1988; Townsend, 1993). Because of its gomphrenoid unilocular anthers, however, the tribe Pseudoplantageae was classified within Gomphrenoideae (Townsend, 1993).

The subtribe Aervinae (Amarantheae, Amaranthoideae) constitutes the most speciose group in the system of Townsend (1993), consisting of 38 genera out of a total of 69 distinguished by him. It has been circumscribed based on inverted seeds and an ascending or superior radicle (Schinz, 1893), although the group otherwise appears morphologically highly divergent. Bentham and Hooker (1880) and Schinz used the name Achyranthinae instead of the older subtribal name "Aerveae" (Endlicher, 1837), which was reestablished by Townsend (1993) using the modern suffix. Subtribe Amaranthinae was diagnosed based on the occurrence of erect seeds and an inferior radicle (Schinz, 1893). Celosieae are characterized by multiovulate ovaries and have remained stable in circumscription since Endlicher (1837).

Genera described or resurrected since Townsend's (1993) treatment mostly belong to Gomphrenoideae (*Hebanthe* Mart., Borsch & Pedersen, 1997; *Pedersenia* J. Holub, a new name for *Trommsdorffia* Mart., Holub, 1998; *Quaternella* T. M. Pedersen, Pedersen, 1997; *Hebanthodes* Pedersen, Pedersen, 2000), while only a few belong to Amaranthoideae (*Omegandra,* G. J. Leach et al., 1993; *Lecosia* T. M. Pedersen, Pedersen, 2000). Generic limits have historically fluctuated greatly, sometimes leading to extreme numbers of generic synonyms, as for ex-

ample in *Alternanthera porrigens* Kuntze (historically also treated as *Achyranthes* L., *Brandesia* Mart., *Celosia* L., *Gomphrena*, *Illecebrum* Spreng., *Mogiphanes* Mart., and *Telanthera* R. Br.; Borsch, 1993). This fluctuation was due to the varying interpretation of floral characters, principally presence and shape of pseudostaminodia and lateral stamen appendages in the androecium, without a complete understanding of the developmental patterns. This fact was succinctly discussed by Eliasson (1988), who assumed that androecium characters may be easily transformed into each other, resulting in difficult homology assessment and unclear delimitation of characters and their states.

In light of the difficulty of interpreting floral morphology, an SEM survey of pollen in Amaranthaceae was undertaken (Borsch, 1998), and it indicated that pollen characters would be potentially very informative for reconstructing phylogenetic relationships in the group. The distribution of newly identified pollen types among taxa implied that most of the units in current and previous classification systems are not natural groups. An extensive molecular analysis of Amaranthaceae based on *rbc*L (Kadereit et al., 2003) corroborated many of the suggestions made in the palynological study. According to the *rbc*L analysis, which mainly aimed at tracing the evolution of C_4 photosynthesis in the Amaranthaceae–Chenopodiaceae alliance, only subfamily Gomphrenoideae and tribe Celosieae of Amaranthaceae were supported as monophyletic, while Amaranthoideae were found to be paraphyletic, and Amarantheae, Amaranthinae, Aervinae, Gomphreneae, Gomphreninae, and Froelichiinae were polyphyletic. In line with the aims of that study, *rbc*L analysis sorted out major lineages of Amaranthaceae, while poor resolution and statistical support left many relationships between and within the main clades unclear.

Interestingly, morphological evidence supporting the position of the first branching taxa (e.g., *Bosea*) and of many genera from the Aervinae in the *rbc*L tree is scarce or entirely lacking. This also explains why these nodes were not reflected by previous classification systems. As a consequence of such unpredictable findings, a dense sampling will be required to gain a fundamental understanding of the evolution of Amaranthaceae.

Apart from the above-mentioned analyses of *rbc*L and *ndh*F (Kadereit et al., 2003; Pratt, 2003), the only recently published evolutionary studies that deal with Amaranthaceae focus on the genus level or below. In *Amaranthus*, questions regarding the evolution of dioecy have been addressed in a recent study on inbreeding depression in the genus (Bram, 2002), and several population-level markers have been used to unravel relationships of cultivated and wild forms (Xu & Sun, 2001). In the same genus, adaptation to a weedy habit has been investigated (Pratt & Clark, 2001). In *Tidestromia*, speciation in deserts of northern Mexico and the southwestern U.S.A. has been addressed (Sánchez-del Pino & Flores Olvera, 2002). Finally, inter-Simple Sequence Repeat markers have been used to infer biogeographic affinities of central and marginal populations of *Froelichia floridana* (McCauley & Ballard, 2002; see also McCauley & Ungar, 2002).

Current Knowledge on Morphology, Anatomy, and Phytochemistry in Amaranthaceae

A survey of pollen morphology in Amaranthaceae (Borsch, 1998) revealed a remarkable diversity and many clearly distinguishable pollen types. It also led to the recognition of metareticulate pollen (Borsch & Barthlott, 1998) and suggested the utility of pollen characters for reconstructing phylogenetic relationships in the family, with many pollen types probably being synapomorphies for genera or groups of genera. For some complex pollen characters, however, such as stellate pore ornamentation (Livingstone et al., 1973), two or more parallel evolutionary events were hypothesized. So far, the analysis of pollen morphology has been restricted to characters that can be illustrated using SEM and LM. The early work of Roland (1971) only depicts manually drawn diagrams of the ultrastructure of *Celosia* and is therefore of limited value. A TEM survey of the ultrastructure of pollen walls in centrospermous families (Skvarla & Nowicke, 1976) included three genera of Amaranthaceae, but they utilized the acetolysis method (Erdtman, 1960), which did not yield as much information as more recent methodologies as applied by, e.g., Weber et al. (1999).

Beyond pollen morphology, current knowledge on morphological and anatomical characters in Amaranthaceae has often been restricted to narrowly circumscribed groups of closely related species or extended to morphological characters that can rather easily be described, as they have been used in monographic treatments (Schinz, 1934) and floras.

A survey of stem and wood anatomy in Amaranthaceae is available (Carlquist, 2003), although only little can be learned about the systematics of the family from this examination owing to the limited number of species included. Additional data have been compiled by the same author for related

taxa of Caryophyllales (Carlquist & Boggs, 1996; Carlquist, 1998, 1999a, b, c, 2000, 2001), providing a valuable source of comparable data for future broad-scale investigations on the evolution of wood and stem anatomy in the order. In Amaranthaceae, stem anatomy has additionally been studied in two species of *Alternanthera* (Bona & de Morretes, 1997; Rajput & Rao, 2000), in *Aerva* (Rajput, 2001), *Achyranthes* (Rajput & Rao, 2000), *Celosia* (Rajput, 2001), and *Amaranthus* (Campos Viana, 1992; Costea & DeMason, 2001). In the latter genus, more comprehensive morphological investigations of individual species exist (Speranza & Bignami, 1997), and the systematic significance of anatomical stem characters has been addressed (Costea & DeMason, 2001). Apart from this, arbuscular mycorrhizae and root cap cells have been investigated in four species of Amaranthaceae (Arriola et al., 1997).

At the cellular level, sieve element plastids have been studied extensively (Behnke, 1976, 1994) for 15 genera of Amaranthaceae and proved rather uniform within the family. Twelve genera of Amaranthaceae have been screened for epicuticular waxes, but none were found (Barthlott, 1994). Trichomes, which have played an important part in taxonomic treatments (e.g., Ulbrich, 1934), have been studied in detail for Amaranthaceae and Chenopodiaceae (Carolin, 1983), and 10 main trichome types occurring in the alliance have been identified. With respect to its taxonomic implications, floral morphology has been considered in some detail for New World taxa of Amaranthaceae (Eliasson, 1988). For *Pleuropetalum*, even details on the floral development are known (De Craene et al., 1999). Aside from this, the most comprehensive review of morphology and anatomy of Amaranthaceae remains that of Schinz (1934). Cytological data are available for different genera of Amaranthaceae (Sharma & Banik, 1965), but the limited sampling prohibits phylogenetic conclusions.

Beyond the characteristic occurrence of betalain pigments (Mabry & Dreiding, 1968; reviewed in Clement et al., 1994), a number of interesting phytochemical compounds have more recently been found and studied in Amaranthaceae, such as methylenedioxyflavonols (Ferreira & Dias, 2000), saponins (Young et al., 1997; Marouf et al., 2001; Mitaine-Offer et al., 2001), (Nor-) triterpenoids (Shiobara et al., 1993), ecdysteroids (Shiobara et al., 1993; Savchenko et al., 1998), specific root-located carbohydrates (Vieira & Figueiredoribeiro, 1993; Shiomi et al., 1996), and various others (Salvador et al., 2002; Alam et al., 2003; De Oliveira et al., 2003). The distribution of phytoecdysteroids, studied in more detail in *Gomphrena* (Savchenko et al., 1998), might prove useful for infrageneric delimitations in the genus, in particular since evidence for its polyphyly exists based on previous palynological (Borsch, 1998) and molecular data (Kadereit et al., 2003).

Classification and Relationships within Chenopodiaceae

Since the focus of this study is on Amaranthaceae, the presentation of Chenopodiaceae systematics at this point is kept to the level of major groups. For the Chenopodiaceae, the largest sampling so far compiled is that of the recent *rbc*L analysis (Kadereit et al., 2003). For details on the history of classification of the chenopodiaceous lineages we refer to this paper. In the context of studying the Amaranthaceae s. str., considerable insights into Chenopodiaceae phylogeny are needed to test the monophyly of the Amaranthaceae and to assess which of the lineages in Chenopodiaceae are their closest relatives.

Aims of This Study

Using the densest sampling so far obtained for Amaranthaceae s. str. and a representation of all major lineages of Chenopodiaceae found by *rbc*L sequence data (Kadereit et al., 2003), our primary goals were to test the monophyly of Amaranthaceae, to investigate relationships of the family to Chenopodiaceae, and to resolve phylogenetic relationships within Amaranthaceae.

Previous studies have substantiated the utility of the *trn*K intron and *mat*K gene for resolving phylogenetic relationships in a broad taxonomic range (Steele & Vilgalys, 1994; Johnson & Soltis, 1995; Hilu & Liang, 1997; Meimberg et al., 2000, 2001; Cuénoud et al., 2002; Hilu et al., 2003), and patterns of variability that may be responsible for this have been studied in detail (Hilu, Müller & Borsch, in prep.; Müller & Borsch, 2005; Hilu et al., 2003). Therefore, the complete *trn*K intron, including *mat*K, was sequenced for representatives of all previously identified lineages (Kadereit et al., 2003) and suprageneric taxa (Townsend, 1993) in Amaranthaceae. To additionally address the relationships between Chenopodiaceae and Amaranthaceae on the one hand, and between the ACA clade and the core Caryophyllales on the other, a relatively high number of species from Chenopodiaceae (representing all tribes, Kühn et al., 1993) and other Caryophyllales were sampled as well.

Our ongoing studies on Amaranthaceae were also initiated with the aim to analyze evolution of tri-

colpate-derived pantoporate pollen in a suitable exemplar family. Pollen characters have proven to be even more promising for systematics of angiosperms on more diverse taxonomic levels than previously acknowledged. Pantoporate pollen, however, has never been analyzed in a phylogenetic framework; there exist detailed evolutionary studies only for monosulcate-derived pollen, utilizing DNA-based phylogenies (e.g., Doyle et al., 2000; Furness & Rudall, 2003; Harley & Baker, 2001; Sauquet et al., 2003). Reasons for choosing Amaranthaceae as such a model case for studying pollen evolution in more detail are diverse. Together with Chenopodiaceae, they form the largest angiosperm lineage with exclusively pantoporate pollen and exhibit a vast range of aperture numbers from few to what may be the highest in angiosperms (250 in *Froelichia floridana*, Borsch, 1998), making the family ideal for exemplarily studying the evolution of pantoporate pollen. Furthermore, Amaranthaceae feature C_4 metabolism and specialized reproductive systems that enabled them to inhabit extreme habitats, ranging from aquatic to xerophytic, and to become distributed worldwide (Borsch et al., 2001).

Also in this study, character evolution will be traced on an independently derived tree for six selected morphological characters that have been used for tribal and subfamilial classification in traditional systems (Table 1; e.g., ovule number) or are presumed to be valuable in inferring phylogenies (pollen characters).

Material and Methods

Material

The complete *trn*K intron of 74 species of Amaranthaceae, Chenopodiaceae, and representatives of other Caryophyllales families was analyzed. Sampling aimed at including previously established lineages (Kadereit et al., 2003) as well as representing all currently accepted subtribes according to Schinz (1934) and Townsend (1993). Material was either collected during fieldwork in North America and South Africa, obtained on loan from different herbaria or from colleagues, or it was taken from the living collection of the Botanical Gardens in Bonn, Germany. Sequences of several species were downloaded from GenBank (cf. Table 2). All species, their respective families, infrafamilial classification, sources of material, and voucher/accession numbers are listed in Table 2.

DNA Isolation, Amplification, and Sequencing

Total genomic DNA was isolated from fresh material, silica-gel-dried leaves, or herbarium specimens. DNA isolation followed a modified triple-extraction approach with CTAB as described in Borsch et al. (2003).

The *trn*K intron was amplified and sequenced using the primers given in Table 3. In most cases, two overlapping halves of the sequenced regions were amplified. The high variability of the *mat*K coding region necessitated the design of many internal amplification and sequencing primers, which was facilitated by the program SeqState developed in this study (Müller, 2003b). Purification of genomic DNA was achieved using QiaQuick columns (Qiagen Inc., Valencia, California). PCR reactions were performed in 25 µl reactions containing 1 U *Taq* DNA polymerase (Promega), 1 mM dNTP mix (1.25 mM each), 1 × buffer (Promega), 1.5 mM $MgCl_2$, and 0.4 µM of each amplification primer. Amplification conditions were: 34 cycles of 94°C (1 min.) denaturation, 52°C (1 min.) annealing, 72°C (2 min.) extension, and 72°C (15 min.) final extension. PCR products were then purified using a QiaQuick gel extraction kit (Qiagen Inc., Valencia, California) and directly sequenced with the ABI Prism™ BigDye Terminator Cycle Sequencing Ready Reaction Kit (Perkin Elmer, Norwalk, Connecticut) on ABI 310 or 377 automated sequencers.

Sequence Alignment and Indel Coding

Sequences were manually aligned in the alignment editor QuickAlign (Müller & Müller, 2003), following alignment rules according to Graham et al. (2000) and Borsch et al. (2003). These rules allow an unambiguous homology assessment in regions with indels. In the present data set, alignment was straightforward, since most indels were "entire" indels (following the terminology of Borsch et al., 2003) caused by single, non-overlapping microstructural changes. Regions of ambiguous alignment (mutational hotspots) were excluded from the phylogenetic analysis. The alignment is available from the corresponding author upon request. Indels from the unambiguously aligned regions (for a list see Appendix I) were coded as binary present/absent characters or multistate characters and compiled in a separate matrix (Appendix II) that was combined with the sequence matrix, thereby weighting indel characters equal to substitutional characters. Since homonucleotide strands (microsatellites; here occurring within the excluded hotspots) often vary on the population level, they were not coded here because no information about those polymorphisms is available and length differences might not be representative for the species included.

Table 2. Taxa sampled in the present study. Vouchers and GenBank accession numbers for the sequences generated in this study are provided. Classification followes Townsend (1993) for Amaranthaceae, Kühn et al. (1993) for Chenopodiaceae, Bittrich (1993) for Caryophyllaceae, and the Angiosperm Phylogeny Group (APG, 2003) for the remaining family assignments. For sequences downloaded from GenBank, the reference instead of the voucher specimen is shown as well as the accession number. Herbarium acronyms follow *Index Herbariorum*.

Family, subfamily, tribe	Species	DNA source (Garden/field origin/voucher)	GenBank accession
Amaranthaceae, Amaranthoideae, Celosieae	*Celosia trigyna* L.	Burkina Faso, *Kalheber 161* (FR)	AY514811
	Pleuropetalum sprucei (Hook, f.) Standl.	Hilu et al. (2003)	AF542596
	Hermbstaedtia glauca (Wendl.) Rchb. ex Steud.	Namibia, *C. Neinhuis s.n.* (BONN)	AY514812
	Deeringia amaranthoides (Lam.) Merr.	Guam, Philipp. Sea, *E. Moore 746* (BONN)	AY514814
Amaranthaceae, Amaranthoideae, Amarantheae	*Aerva javanica* (Burm. f.) Juss.	Madagascar, *E. Fischer s.n.* (BONN)	AY514793
	Amaranthus caudatus L.	Bot. Gard. Mainz s.n.	AY514809
	Amaranthus greggii S. Watson	U.S.A., Texas, *D. Pratt, K. Müller & Th. Borsh 207* (ISC, BONN)	AY514808
	Bosea yervamora L.	Canary Islands, Tenerife, *K. Müller 751* BONN	AY514810
	Calicorema capitata (Moq.) Hook. f.	Namibia, *C. Neinhuis s.n.* (BONN)	AY514807
	Chamissoa altissima (Jacq.) HBK var. *altissma*	Paraguay, *E. Zardini & L. Guerrero 42592* (BONN, MO)	AY514857
	Achyranthes aspera L.	Bot. Gard. Bonn, BG Bonn 03616, *K. Müller 900* (BONN)	AY514815
	Charpentiera obovata Gaudich.	U.S.A., Hawaii, *B. A. Prigge 15251* (LA)	AY514855
	Charpentiera ovata Gaudich.	U.S.A., *Hawaii, B. A. Prigge 15252* (LA)	AY514856
	Cyathula prostrata (L.) Blume	Peru, *E. Russo 114* (BONN, Herb. Russo)	AY514862
	Nothosaerva brachiata Wight	Burkina Faso, *Anonymous s.n.* (FR)	AY514806
	Nototrichium humile Hillebr.	U.S.A., Hawaii, *B. A. Prigge 15249* (LA)	AY514816
	Nototrichium sandwicense (Gray) Hillebr.	U.S.A., Hawaii, *B. A. Prigge 15250* (LA)	AY514817
	Pandiaka angustifolia (Vahl) Hepper	Burkina Faso, *J. Müller 324* (FR)	AY514818
	Psilotrichum africanum Oliver	South Africa, *K. Müller 878* (BONN, PRE)	AY514822
	Ptilotus manglesii (lindl.) F. Muell.	Australia, *Th. Borsch 3543* (BONN)	AY514824
	Ptilotus obovatus F. Muell.	[Australia], BG Bonn s.n.	AY514823
	Pupalia lappaceae A. Juss.	Bot. Gard. Bonn, BG Bonn 16784, *Th. Borsch 3544* (BONN)	AY514858
	Sericostachys scandens Gilg & Lopr.	Rwanda, *E. Fischer s.n.* (BONN)	AY514819
Amaranthaceae, Gomphrenoideae, Pseudoplantageae	*Pseudoplantago friesii* Suess.	Argentina, *T. M. Pedersen 15792* (CTES, C)	AY514820
Amaranthaceae, Gomphrenoideae, Gomphreneae	*Alternanthera caracasana* HBK	Hilu et al. (2003)	AF542595
	Alternanthera pungens HBK	U.S.A., Texas, *Th. Borsch, D. Pratt & K. Müller 3449* (ISC, BONN)	AY514795
	Alternanthera sessilis (L.) DC.	Bot. Gard. Mainz s.n.	AY514796
	Blutaparon vermiculare (L.) Mears	U.S.A., Texas, *Th. Borsch, D. Pratt & K. Müller 3444* (ISC, BONN)	AY514798

Table 2. Continued.

Family, subfamily, tribe	Species	DNA source (Garden/field origin/voucher)	GenBank accession
	Froelichia floridiana (Nutt.) Moq.	BG Bonn 03615-90, *Th. Thiel s.n.* (BONN)	AY514799
	Gomphrena haageana Klotzsch	Bot. Gard. Mainz	AY514800
	Gomphrena mandonii R. E. Fr.	Bolivia, *S. Beck 18720* (BONN, LPB)	AY514801
	Gomphrena macrocephala A. St.-Hil.	Paraguay, *E. Zardini* 45564 (BONN, MO)	AY514802
	Guilleminea densa (Willd.) Moq.	U.S.A., Texas, *Th. Borsch, D. Pratt & K. Müller 3437* (ISC, BONN)	AY514803
	Hebanthe occidentalis (R. E. Fr.) Borsch & Pedersen var. *occidentalis*	Paraguay, *E. Zardini 45377* (BONN, MO)	AY514821
	Iresine lindenii Van Houtte	Bot. Gard. Mainz s.n.	AY514805
	Iresine palmeri S. Watson	U.S.A., Texas, *Th. Borsch, D. Pratt & K Müller 3445* (ISC, BONN)	AY514804
	Tidestromia lanuginosa (Nutt.) Standl.	U.S.A., Texas, *Th. Borsch, D. Pratt & K. Müller 3439* (ISC, BONN, MEXU)	AY514797
Chenopodiaceae, Chenopodioideae, Atripliceae	*Atriplex elegans* (Moq.) D. Dietr.	U.S.A., Texas, *Th. Borsch, D. Pratt & K. Müller 3425* (ISC, BONN, KAS)	AY514830
	Spinacia oleracea L.	Zurawski et al. (1982)	AJ400848
Chenopodiaceae, Chenopodioideae, Beteae	*Beta vulgaris* L.	Germany, Baltic Sea, *G. Kadereit 99/255* (MJG)	AY514832
	Acroglochin chenopodioides Schrad.	BG Kassel ex BG Lyon, *Anonymous s.n.* (KAS)	AY514826
	Hablitzia tamnoides M. Bieb.	*Th. Borsch 3546*; BG Bonn 3609-90 (BONN)	AY514825
	Aphanisma blitoides Nutt. ex Moq.	U.S.A., California, S. Junak SR-987 (SBBG)	AY514844
Chenopodiaceae, Chenopodioideae, Camphorosmeae	*Bassia hirsuta* (L.) Aschers.	U.S.A., Texas, *Th. Borsch, D. Pratt & K. Müller 3430* (ISC, BONN)	AY514831
	Camphorosma monspeliaca L.	Kasakhstan, Prov. Gur'yev (Atyrau), Makhambat, *H. Freitag 28.133* (KAS)	AY514829
Chenopodiaceae, Chenopodioideae, Chenopodieae	*Chenopodium acuminatum* Willd.	Mongolia, *M. Azuma s.n.* 28.11.1984 (FR)	AY514836
	Chenopodium bonus-henricus L.	Bot. Gard. Mainz, without voucher	AY514834
	Chenopodium botrys L.	Germany, *T. Gregor & S. Demuth, 16.07.1992* (FR)	AY514835
Chenopodiaceae, Chenopodioideae, Camphorosmeae	*Agriophyllum squarrosum* (L.) Moq.	SE Russia, Prov. Astrakhan, *H. Freitag 28.196a* (KAS)	AY514827
	Corispermum ladakhianum C. Grey-Wilson & B. M. Wadhwa	Bot. Gard. Mainz s.n.	AY514837
Chenopodiaceae, Polycnemoideae, Polycnemeae	*Nitrophila occidentalis* S. Watson	U.S.A., Utah, *D. Pratt 204* (ISC, BONN)	AY514840
	Polycnemum majus A. Braun	Bot. Gard. Mainz s.n.	AY514839
	Polycnemum verrucosum Lang	Turkey, *KP Buttler 15976* (FR)	AY514838
Chenopodiaceae, Salicornioideae, Halopeplideae	*Allenrolfea vaginata* (Grisb.) Kuntze	BG Bonn 2488	AY514828
Chenopodiaceae, Salicornioideae, Salicornieae	*Halocnemum strobilaceum* (Pall.) M. Bieb.	Turkey, *H. Freitag & Adigüzel 28.783* (KAS, GAZI)	AY514842

Table 2. Continued.

Family, subfamily, tribe	Species	DNA source (Garden/field origin/voucher)	GenBank accession
Chenopodiaceae, Salsoloideae, Salsoleae	*Salsola kali* L.	Graswarder, Baltic Sea Coast, Germany, *G. Kadereit 1999/211* (MJG)	AY514843
Chenopodiaceae, Salsoloideae, Suaedeae	*Suaeda* cf. *calceoliformis* (Hook. f.) Moq.	U.S.A., Texas, *Th. Borsch, D. Pratt & K. Müller 3440* (ISC, BONN)	AY514841
	Bienertia cycloptera Bunge	Iran, Kavir protected area near Mobarakiyeh, *H. Akahani s.n.*, 16.11.2000 (Hb. Akhani, KAS)	AY514833
Achatocarpaceae	*Achatocarpus praecox* Griseb.	Argentina, *B. Leuenberger, Arroya-Leuenberger & U. Eggli 4345* (B), Bot. Gard. Berlin (142-78-94-10)	AY514845
	Phaulothammnus spinescens A. Gray	Hilu et al. (2003)	AY514846
Cactaceae	*Pereskia zinniiflora* DC.	Nyffeler (2002)	AY01533
	Rhipsalis floccosa Salm-Dyck	Nyffeler (2002)	AY01534
Caryophyllaceae, Alsinoideae	*Scleranthus perennis* L.	Germany, *Th. Borsch 3389* (BONN)	AY514847
Caryophyllaceae, Paronychioideae	*Illecebrum verticillatum* L.	Germany, *Th. Borsch & K. Müller 3541* (BONN)	AY514849
Caryophyllaceae, Caryophylloideae	*Silene otites* Sm.	Netherlands, *Th. Borsch 3495* (BONN)	AY514848
Halophytaceae	*Halophytum ameghinoi* Speg.	Sukkulentensammlung Zürich s.n.	AY514852
Portulacaceae	*Anacampseros vulcanensis* Añon	Hilu et al. (2003)	AF542597
	Talinum paniculatum (Jacq.) Gaertn.	Nyffeler (2002)	AY015274
	Talinella sp. indet.	*Röösli s.n.* (BONN)	AY514859
Phytolaccaceae	*Rivina humilis* L.	BG Bonn 9865, *Th. Borsch 3542* (BONN)	AY514850
Drosophyllaceae	*Drosophyllum lusitanicum* (L.) Link	BG Bonn 09015	AY514860
Frankeniaceae	*Frankenia laevis* L.	BG Bonn s.n., *K. Müller 884* (BONN)	AY514853
Plumbaginaceae	*Limonium latifolium* (Sm.) Kuntze	BG Bonn 03678, *K. Müller 883* (BONN)	AY514861
Simmondsiaceae	*Simmondsia chinensis* (Link) C. K. Schneid.	Bot. Gard. Bonn 310700001	AY514854

PHYLOGENETIC ANALYSIS

Maximum Parsimony

Maximum parsimony analysis (MP) was conducted using PAUP*4b10 (Swofford, 1998) and PRAP (Müller, 2003a), which generates command files for PAUP* that allow parsimony ratchet searches (Nixon, 1999). Ten random addition cycles of 200 ratchet iterations each were applied. Iterations comprised two rounds of TBR branch swapping each, one on a randomly reweighted data set (25% of the positions), and the other on the original matrix, saving one shortest tree. Since each random addition cycle converged to the same tree score soon, cycles were not extended to more than 200 iterations, nor were further cycles added. Shortest trees collected from the different tree islands were used to compute a strict consensus tree. Statistical support was estimated by bootstrapping, saving up to 100 trees in each of 500 replicates. The calculation of Bremer support also applied the parsimony ratchet algorithm (see Müller, 2004), again with help of PRAP. The consistency index CI (Kluge & Farris, 1969) and rescaled consistency index RC (Farris, 1989) were calculated to assess homoplasy.

Maximum Likelihood

The model of molecular evolution applied in the maximum likelihood analysis (ML) was tested using the Akaike information criterion (AIC, Akaike, 1974), which rewards models for good fit but imposes a penalty for surplus parameters that may increase both computational effort and sensitivity

Table 3. Primers used for sequencing the *trn*K intron in the Caryophyllales.

Name	Position in alignment (bp)[2]	Sequence[1]	Source
For amplification of the whole intron:			
*trn*KFbry	Upstream of matrix	ATCATGGGGTTGCTAACTCA>	Quandt (pers. comm.)
*trn*K 3914Fdi	Upstream of matrix	GGGGTTGCTAACTCAACGG>	Johnson & Soltis (1995)
*trn*K 2R	Downstream of matrix	<CTACTCCATCCGACTAGTT	Johnson & Soltis (1995)
MG1	Downstream of matrix	<ATCTACTCCATCCGACTAGTT	Liang & Hilu (1996)
For amplification of parts of the intron and for sequencing:			
ACmatK1200R	1308	<GTGTTAGATATATTAATACCT	This study
ACmatK873R	909	<CCACTTCTCTTTCAGGAGTATAT	This study
ACmatK490F	1390	CTGGTTGAAAGATGCTTCKTC>	This study
ACmatK100F	1062	CTCGACTGTATCAACAGAATC>	This study
ACmatK871R	905	<CTATCCACTTATCTTTCAGGAATA	This study
ACmatK1426R	1461	<CCAAAAGAATCCATTTCCTTT	This study
NymatK480F	1356	CATCTGGAAATCTTGSTTC>	Borsch (2000)
ACmatK499F	1405	CCTCKTCTTTGCATTTATTACG>	This study
ACmatK2080R	2101	<ATATTATTGACCGATTTGGAC	This study
ACmatK500F	1405	TTCTTCTTTGCATTTATTACG>	This study
ACmatK650r	1526	<CYATGTATGTGAATATGAATCC	This study
ACmatK1983F	2002	TAAAAAATTCGATACCATAGTTCC>	This study
ACmatK1252R	1272	<CCTTTTTTAGAGGATCAATTCTCA	This study
ACmatK200r	1158	<GCAGTCATTGTGGAAATTC	This study
ACmatK1300R	2209	<GTGCTAGAACTTTGTCTCGYA	This study
ACmatK1250F	2161	CTCATTATTATAGTGGCTCYTC>	This study
ACmatK1809F	1842	AATGTTATTTTTCTGTGTGGTCTC>	This study
ACmatK2149F	2182	CTCAAGAAAAAAAAGTTTGTATCG>	This study
ACmatK975F	1033	ATACAGTTTACTAATWGTRAAACG>	This study
ACmatK1400R	1529	<TGTATGTGAATACGAATCC	This study
ACmatK700R	1611	<GAACGAATMCATTTCTACGGA	This study

[1] Sequences starting with "<" are reverse primers as aligned in a 5′ → 3′ alignment. The oligonucleotide actually used is the reverse complement of the sequence shown. Sequences ending with ">" are forward primers.
[2] First nucleotide of primer head.

to random error (Swofford et al., 1996; Posada & Crandall, 1998). AIC values were calculated and the optimal model was selected using Modeltest 3.06 (Posada & Crandall, 1998). The substitution model of the general time reversible model (GTR) (Rodriguez et al., 1990) was chosen in which the two transitional rates are united (TVM, Posada & Crandall, 1998). Additional hierarchical likelihood ratio tests were also performed with Modeltest. The assumption of two unequal transitional rates yielded an insignificant increase of likelihood scores over the null hypothesis of equal transitional rates ($P \gg 0.01$). Moreover, among-site rate variation following a gamma distribution (estimated shape parameter, four rate categories represented by the mean) and an estimated proportion of invariable sites had to be assumed according to the AIC (GTR + G + I). The final maximum likelihood analysis was conducted with PAUP*4.0b10 (Swofford, 1998), starting TBR branch swapping on one of the shortest trees found with Maximum parsimony.

Bayesian Inference

Bayesian inference of phylogeny (BI) was performed using the program MrBayes (Huelsenbeck & Ronquist, 2001). As in the likelihood analysis, the GTR model of nucleotide substitution was employed, assuming site-specific rate categories following a gamma distribution. The a priori probabilities supplied were those specified in the default settings of the program. Posterior probability (PP) distributions of trees were created using the Metropolis-coupled Markov chain Monte Carlo method and following previously suggested search strategies (Huelsenbeck & Ronquist, 2001; Huelsenbeck et al., 2001; Huelsenbeck et al., 2002). Only PPs of 95% or higher were considered significant (alpha = 5% = 0.05), in particular in view of the frequently reported tendency toward overcredibility of posterior probabilities relative to bootstrap frequencies (Suzuki et al., 2002; Erixon et al., 2003). Four chains were run simultaneously, with the tempera-

ture set to 0.2. Chains were sampled every 10 generations and the respective trees were written to a tree file. This was repeated three times, comprising one million generations. All three runs started from different random tree topologies. In all cases, the probabilities converged onto the same stable value around generation 40,000. Calculation of the consensus tree and of the posterior probability of clades was done for all three runs, based upon the trees sampled after the burn-in. Consensus tree topologies based on the different analyses were found to be identical. The posterior probabilities diverged only slightly at a few nodes, so that those of only one arbitrarily chosen BI tree are provided below.

TRACING THE EVOLUTION OF SELECTED MORPHOLOGICAL CHARACTERS

Six selected morphological characters were compiled into a small data matrix, using information obtained from the literature or through direct observation of specimens. The character evolution was traced on the tree derived from maximum likelihood analysis (Fig. 2) using Mesquite 1.0 (Maddison & Maddison, 2003). Due to difficulties in assessing homology across families for character six, the architecture of partial inflorescences, coding of this character was restricted to Amaranthaceae. Unambiguous character state transformations and those obtained when accelerated or delayed transitions are assumed were visualized using WinClada (Nixon, 1996) and finally plotted on a simplified tree with TreeGraph (Müller & Müller, 2004) (see caption of Fig. 4 for more details). This data matrix is provided in Appendix III.

Results

PATTERNS OF VARIABILITY OF *trn*K/*mat*K IN CARYOPHYLLALES

From the raw data matrix (3196 positions), six hotspot regions (bp 394–408; 583–618; 670–773; 972–1024; 2874–2901; 3067–3105) had to be excluded due to unattainable primary homology assessment. In addition, bp 3165–3196 (3′ end) were removed due to the accumulation of missing data caused by varying primer read starts. The resulting matrix was used during the analyses and comprised a total of 2875 characters, out of which 1599 were contributed by the *mat*K coding region, 860 by 5′ noncoding intron part, and 417 by the 3′ noncoding intron part. The actual sequence length of the *trn*K intron ranged from 2378 to 2644 bp among the taxa sampled. An overall uncorrected sequence divergence of 10% yielded a total of 39% of parsimony informative (57% variable) positions for the whole intron. The *mat*K coding region exhibits 45% parsimony informative (66% variable) characters, while the 5′ and 3′ noncoding intron parts comprise 35% (51%) and 25% (35%) parsimony informative (variable) sites. As previously observed in *mat*K data sets (Hilu & Liang, 1997; Soltis & Soltis, 1998; Hilu et al., 2003), the overall transition/transversion ratio was close to one (1.2). These and additional sequence statistics are provided for both non-coding regions and the *mat*K-coding region separately in Table 4.

There were 175 insertion/deletion events identified and coded (Appendices I and II). Inversions were found in *Halophytum* Speg. and *Rhipsalis floccosa*. Because of a palindromic region, the actual size of the inversion could not be exactly inferred, but apparently ranges from a minimum of four Adenins (from character no. 1898 to 1907) to a maximum of 24 bp (from bp 1888 to 1917). A further inversion was recognized in *Drosophyllum* Link, with a maximum possible extension from bp 192 to 247 (30 bp) or a minimum extension from 202 to 233 (14 bp). For inversions, different possibilities exist with regard to their alignment and treatment during analysis. Obviously, the inverted block (of one or more sequences) could be separated from the uninverted block in the alignment, thus avoiding an erroneous inference and overweighting of substitutions (see discussion in Quandt et al., 2003). Here, we adopted the alternative handling of reverse complementing one of the two corresponding blocks and thereafter treating the positions of the uninverted and the reverse-complemented, formerly inverted sequence parts as homologous.

RESULTS OF THE PHYLOGENETIC ANALYSES

When parsimony analyses were based on substitutions only, the shortest trees found had 5360 steps and a CI of 0.487, an RI of 0.656, and an RC of 0.320. The strict consensus tree is shown in Figure 1, together with bootstrap (above branches) and Bremer support (italicized, below branches, left number). Following common practice in interpreting non-parametric bootstrap values (cf. Soltis et al., 2000), nodes with 85% or higher are regarded as well supported.

When indel information was included, the length of the shortest trees rose to 5574 steps (CI = 0.501, RI = 0.664, and RC = 0.333). The tree topology was identical to that from the analysis without indels shown in Figure 1. On average, support increased slightly compared to the analyses without

Table 4. Sequence statistics for the *trn*K intron in Caryophyllales. Characters = number of characters in the alignment matrix (excluding hotspots and coded indels); Length range = actual sequence length in nucleotides (including hotspots; minimal and maximal value observed); S.D. = standard deviation of mean length; % divergence (range) = pairwise sequence distance in percent (uncorrected p distance, overall mean, lowest and highest scores in brackets); ti/tv ratio (transition/transversion ratio based on p distances; range in brackets); % variable = percentage of variable positions; % informative = percentage of parsimony informative positions; % GC = GC content.

Region	Characters	Length range	Mean length	S.D.	% divergence	ti/tv ratio	% variable	% informative	%GC
*trn*K intron	2875	2378–2644	2463.2	37.3	10.1 (0.3–22.5)	1.2 (0.1–2.2)	56.8	38.8	32.8
noncoding 5′ intron part	860	625–739	707.4	18.3	9.8 (0.2–24.1)	1.4 (0.0–9.0)	50.7	34.7	34.1
*mat*K	1599	1503–1539	1517.9	5.8	9.9 (0.3–23.4)	1.2 (0.2–2.4)	65.6	44.7	32.3
noncoding 3′ intron part	417	213–379	237.9	29.0	12.2 (0.0–31.2)	1.1 (0.0–9.0)	35.3	24.5	32.6

indels. Since the deviation was more apparent in the Bremer support values (bootstrap values will soon become saturated; Bremer, 1994), these are given next to those from the analysis based on substitutions only (italicized, below branches, right number).

The likelihood analysis yielded one optimal tree with a likelihood score of 32150.36646. This tree is shown in Figure 2 with branch lengths optimized according to the model used during reconstruction. The Bayesian approach found the consensus tree and posterior probabilities provided in Figure 3. Accepting a type I error of 5%, only those nodes with 95% or higher will be regarded as well supported in the discussion.

There was no conflict between the trees obtained with the three different methods with one exception. *Iresine* was resolved as monophyletic using parsimony, but not so in the likelihood and Bayesian analyses. However, the respective conflicting nodes were unsupported (according to bootstrap, Bremer support, and posterior probability) and very short branches made up the conflicting part of the likelihood-based topology (Fig. 2). Confidence in other nodes that were resolved in the likelihood-based analysis but not in the parsimony analysis (e.g., subsets of the Achyranthoid clade; Fig. 3b) was also low.

MORPHOLOGICAL CHARACTER MAPPING

A tree that shows character state transformations of six morphological characters is presented in Figure 4. The tree has a reduced number of terminals and summarizes the results of the different analyses, depicting the likelihood-based topologies except for the position of *Iresine*, which is shown in a polytomy (see discussion). For some characters it was not possible to localize unambiguous character state transformations on the tree. For these, the state transformations as inferred assuming accelerated transitions are plotted. In the discussion, more weight will be granted to those inferred transformations that are unambiguous.

DISCUSSION

PHYLOGENETIC INFERENCE: METHODOLOGICAL DIFFERENCES

There was no substantial conflict among the tree topologies obtained with the three different methods, except that *Iresine* was seen to vary, being resolved as monophyletic using parsimony while it appears polyphyletic using likelihood and Bayesian inference. Since the involved branches are unsup-

ported regardless of the statistic invoked and since the respective branches are very short, this conflict cannot be regarded as strong; which points to the fact that more data and/or taxa will be needed to resolve this important part of the tree that potentially links the traditional Amaranthoideae with the Gomphrenoideae. The problems with *Iresine* could also relate to a too sparse sampling. Preliminary studies involving a larger number of *Iresine* species (Borsch, Flores Olvera, Zumaya & Müller, unpublished data) provide evidence for the monophyly of *Iresine* and show that the two included species, *Iresine lindenii* Van Houtte and *Iresine palmeri* S. Watson, represent two distant clades.

For all other parts of the tree, the emerging picture is without conflicts, but nevertheless not always totally clear. This is particularly evident in the Achyranthoid clade (Fig. 3b), which is partly unresolved using the parsimony approach (Fig. 1b). Likelihood and Bayesian inference, however, at least provide a preliminary hypothesis on relationships, but since support is lacking in parts, this will have to be confirmed by future studies that employ a wider sampling of both characters and taxa (Bremer et al., 1999).

To trace the history of character evolution and to discuss the systematic implications, one topology has to be chosen that currently seems to best reflect the true organismal phylogeny. Since our likelihood-based topologies display more resolution while not being incongruent with the parsimony tree (with the exception of *Iresine*), we choose to use them as a basis. As the rise in Bremer support values indicates, indels were found mostly to support some of the most basal nodes such as the Amaranthaceae–Chenopodiaceae alliance or the Amaranthaceae, or terminal nodes like the monophyly of genera, such as *Alternanthera* and *Ptilotus*, alternately. At this point, we prefer not to pay too much attention to the exact position of both *Iresine* species for the reasons given above, but merely state that *Iresine* is part of the more inclusive clade uniting core Gomphrenoids and Achyranthoids (Fig. 3b). This is also reflected in the simplified topology presented in Figure 4. During the discussion, we also reject the significance of those nodes that remain unsupported or weakly supported according to the principles outlined above.

UTILITY OF *trn*K/*mat*K IN ADDRESSING PHYLOGENETIC QUESTIONS IN CARYOPHYLLALES

To date, *mat*K/*trn*K sequence data have frequently proven to provide increased resolution and support on various phylogenetic levels compared to other molecular markers (Hilu & Liang, 1997; Soltis & Soltis, 1998; Hilu et al., 2003). Even when taking the effect of different taxon sampling into account, this trend is also evident in the present study, since large parts of the tree gain higher support and resolution than they did in previous single gene studies in the group (Cuénoud et al., 2002; Kadereit et al., 2003; see Introduction). This may be merely a consequence of a larger number of informative characters (Table 4) compared to similarly sized genes, but also of a different signal quality (i.e., levels of homoplasy). With respect to this effectiveness of *mat*K, similar findings have been made in the overall context of angiosperms (Hilu et al., 2003; Hilu, Müller & Borsch, in prep.). However, a detailed comparison of the different gene tree statistics needs to await a more complete and exactly parallel sequencing of all markers, since tree topology and statistical support are most sensitive to taxon sampling.

MONOPHYLY OF THE AMARANTHACEAE–CHENOPODIACEAE ALLIANCE AND ITS POSITION IN THE CARYOPHYLLALES

Similar to previous reports (Rodman, 1994; Cuénoud et al., 2002; Kadereit et al., 2003; Pratt, 2003), the present study again shows that the Amaranthaceae–Chenopodiaceae alliance constitutes a monophyletic group together with the Achatocarpaceae. The significance of this relationship is substantially increased with *mat*K/*trn*K when studies with a comparable sampling are taken into account (e.g., 80% bootstrap in Kadereit et al. (2003), 98% BS here, 100% PP, 8 Bremer support or decay, DC). Morphological synapomorphies underlining this relationship are currently unknown, although Achatocarpaceae had been previously included in Amaranthaceae (Bentham & Hooker, 1880). Unifying pollen features described (Rodman, 1994) are somewhat blurred by the strongly deviating pollen morphology resulting in a difficult homology assessment in Achatocarpaceae (Nowicke, 1994), which is currently being studied in more detail (Müller & Borsch, unpublished).

Support for the sister group relationship of Caryophyllaceae to the ACA clade continues to be weak to moderate. Based on *rbc*L data, it was less than 50% bootstrap (BS) (Savolainen et al., 2000b), but rose to 73% through a denser sampling (Kadereit et al., 2003). With *trn*K sequence data, support for this relationship is only found in the maximum likelihood and Bayesian analysis (100% posterior probability; PP), but not under parsimony that leaves the ACA clade and the Caryophyllaceae

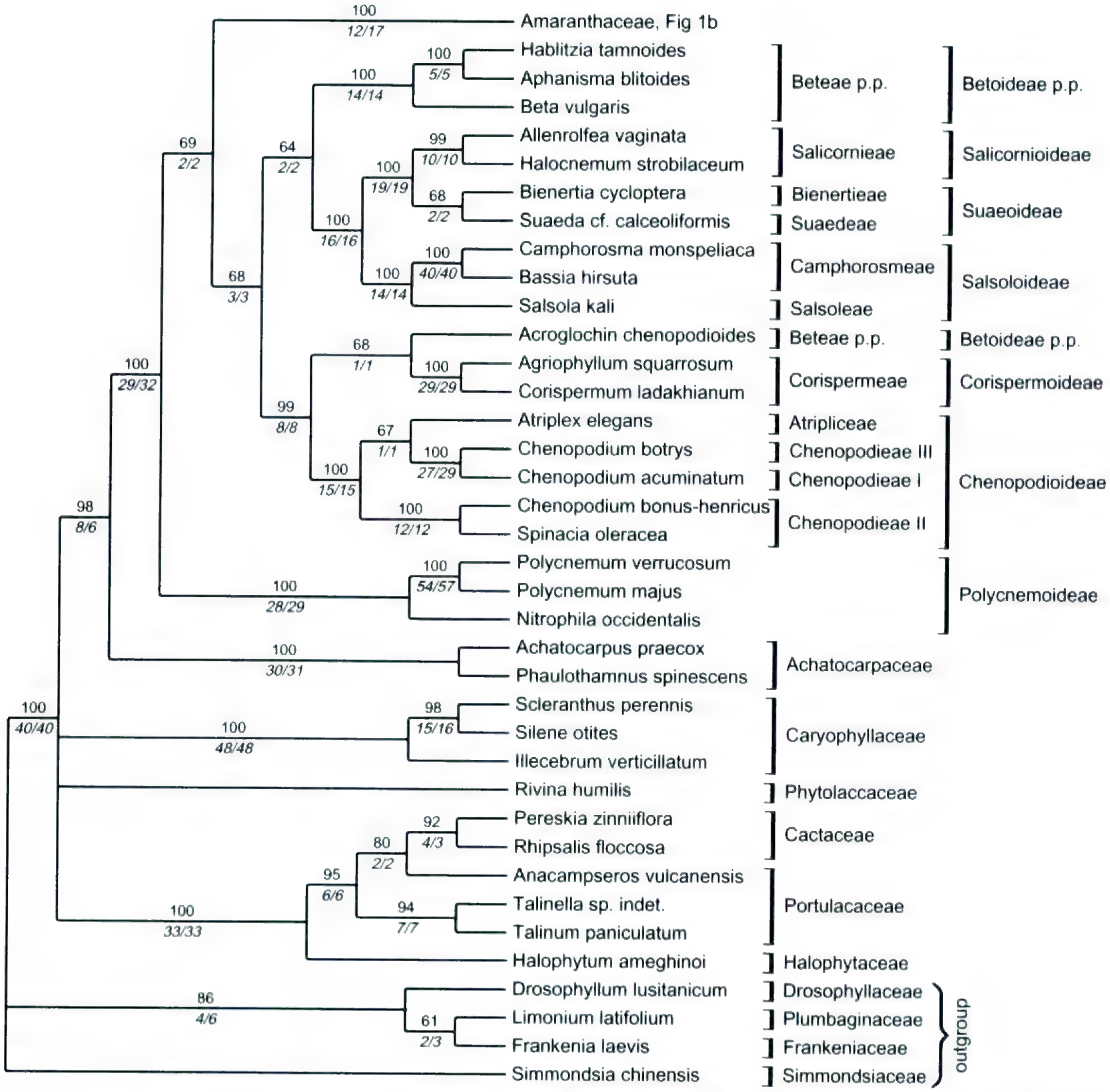


Figure 1 (pages 80–81). Strict consensus tree from the parsimony analyses both with and without inclusion of coded indels (without indels: 5360 steps, CI = 0.487, RI = 0.656, RC = 0.320; with indels: 5574 steps, CI = 0.501, RI = 0.664, RC = 0.333). Bootstrap values are given above branches, and Bremer support below branches (left number = without indels, right number = including indel characters). —a (page 80). Section of the tree focusing on Chenopodiaceae, closely related Caryophyllales, and outgroup. The classification of Chenopodiaceae follows Kühn et al. (1993) and Kadereit et al. (2003). p.p. = *pro parte*.—b (page 81). Section of the tree focusing on Amaranthaceae; the classification follows Townsend (1993). P = Pseudoplantageae; Gomph = Gomphreninae; Froel = Froelichiinae. From left to right, subtribes, tribes, and subfamilies are indicated.

unresolved (Fig. 1a). Since knowledge of the sister group of ACA is central to understanding character evolution in this clade, the present situation points toward the need of increasing character number and/or taxon sampling density. Traditionally, subfamily Paronychoideae of the Caryophyllaceae (also classified as Illecebraceae, Bentham & Hooker, 1880) had been regarded as closely related to the Polycnemoideae (Kühn et al., 1993). The *rbc*L data could not hold up this view (Kadereit et al., 2003) and are compatible with the *trn*K phylogeny presented here.

Amaranthaceae plus Chenopodiaceae together form a well-supported clade with *trn*K evidence (100% BS, 100% PP, 29–32 DC), which is congruent with results from other studies (Giannasi et al., 1992; Rettig et al., 1992; Downie & Palmer, 1994; Rodman, 1994; Downie et al., 1997; Cuénoud et al., 2002; Pratt, 2003; Kadereit et al., 2003). Among these, those with the most extensive and,

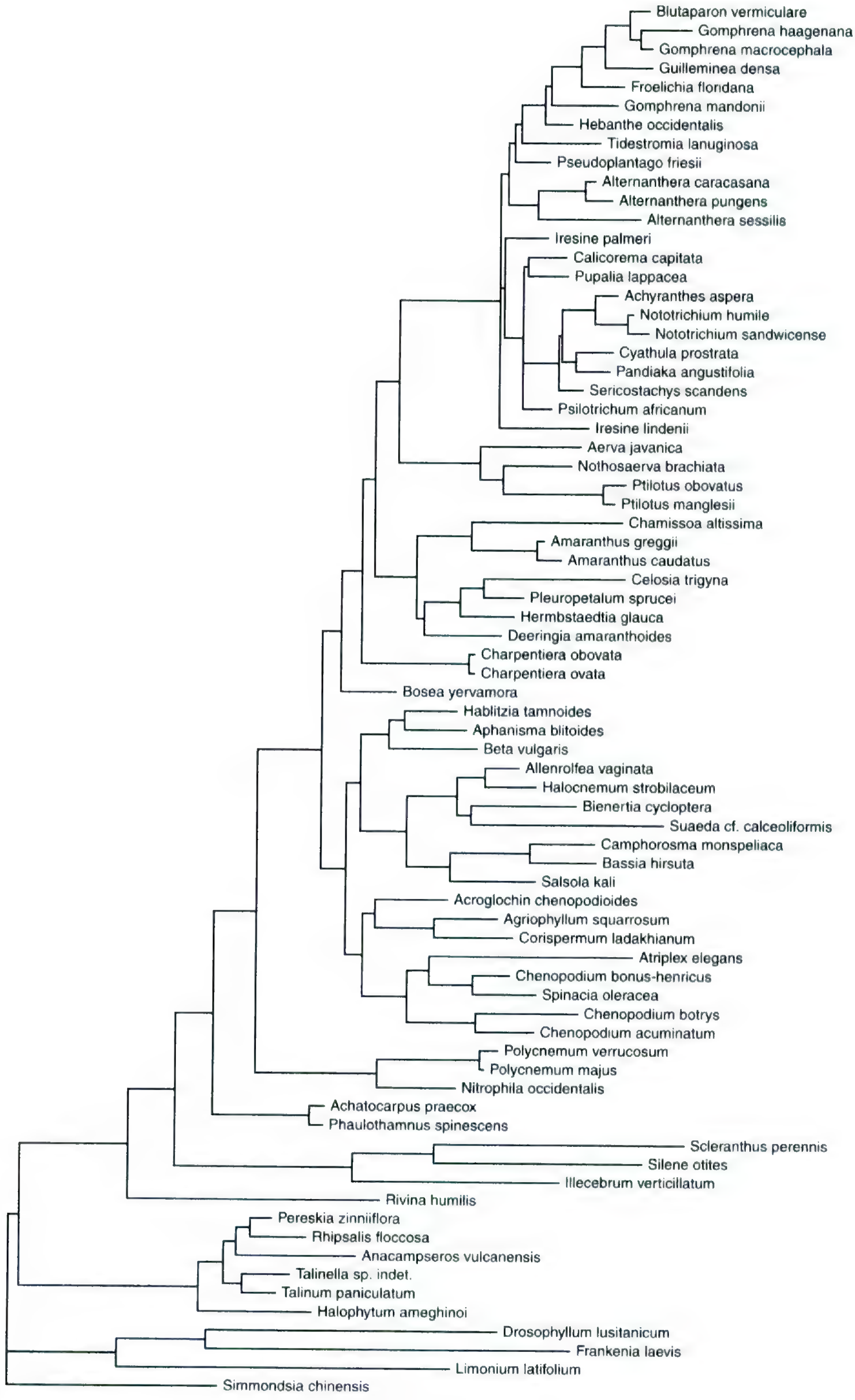


Figure 2. Phylogram derived from the maximum likelihood analysis, illustrating relative branch lengths.

nodes that differ between gene trees but do not gain statistical support in any of these trees so that there is no significant conflict. We reserve "incongruent" for statistically supported differences in topology.

*rbc*L and *ndh*F agree in resolving Polycnemoideae as sister to Amaranthaceae (< 50% with *rbc*L, 66% with *ndh*F). In the present study, Polycnemoideae are sister to a clade of Amaranthaceae plus the remaining Chenopodiaceae (see discussion of chenopodiaceous lineages below). Among the nodes expressing this relationship, the one uniting all Chenopodiaceae except for Polycnemoideae receives only 69% BS and 59% PP. Due to both inconsistency and node instability, it appears that clarifying the relationship between Amaranthaceae and Chenopodiaceae will require more data before a clear picture emerges.

PHYLOGENY OF AMARANTHACEAE

Trees based on *mat*K/*trn*K sequence data clearly show that most of the entities recognized at the tribal or subtribal level by previous authors (Table 1) do not reflect natural groups (plotted in Fig. 1b). Compared to the *rbc*L analysis (Kadereit et al., 2003), the addition of taxa, particularly in the large tribe Amarantheae, has led to an improved understanding of relationships in this study.

The basal grade of Amaranthaceae consists of genera from Amaranthoideae–Amarantheae–Amaranthinae (sensu Townsend, 1993). This is consistent with *rbc*L evidence (Kadereit et al., 2003), but better supported here. In the *rbc*L tree, *Bosea* is resolved in an unsupported trichotomy also comprising Polycnemoideae and the remaining Amaranthaceae, while *Charpentiera* as the second branching taxon in the Amaranthaceae receives 63% bootstrap support. *Bosea* had previously been identified to branch first based on five representatives and partial *mat*K sequence data in a study on Caryophyllales phylogeny (Cuénoud et al., 2002). In a study using *ndh*F sequences (Pratt, 2003), *Charpentiera* diverges first, followed by the Amaranthus/Chamissoa/Celosieae clade and *Bosea*. However, this hypothesis did not receive high support (70%–74% BS), and distance analyses with *ndh*F found a Charpentiera/Bosea clade juxtaposed to the Amaranthus/Chamissoa/Celosieae clade. The extant distribution of these putative basal genera is remarkable, with *Bosea* restricted to Macaronesian islands, Cyprus, and the western Himalayas, and *Charpentiera* to Pacific islands (Hawaii and Tubuai islands). Moreover, *Bosea* and *Charpentiera* share their woody habit with many Celosieae and *Chamissoa*, and *Bosea* seems to be similar in its berry-like fruits to *Deeringia* R. Br. and *Pleuropetalum*. In the present study, support for the nodes in this basal grade is 100, 98, and 100% BS; 12, 4, and 10 DC without indels; and three times 100% PP, respectively (Fig. 1b). Nonetheless, further sampling of genera of the Amaranthinae will be essential to establish the exact branching order at the base of the Amaranthaceae because of the incongruence with other studies. Moreover, it is now clear that Amaranthinae as traditionally circumscribed are paraphyletic and, therefore, still may embrace genera with unforeseen positions in the phylogeny.

A monophyletic Celosieae as sister to an Amaranthus–Chamissoa lineage is in agreement with the *rbc*L and *ndh*F studies as well, but *trn*K data provide more resolution and suggest *Deeringia* as the first branching genus of the tribe. Additional support for the basal position of *Deeringia* comes from a recent study on the tribe using nuclear ribosomal ITS1 and ITS2 sequences with two representatives of *Deeringia* along with 14 species from *Hermbstaedtia*, *Celosia*, and *Pleuropetalum* (Thiel, 2003). The reason for an incongruent position of *Amaranthus* outside the core of Amaranthaceae as indicated by ORF2280 sequences (Downie et al., 1997) might be sought in the restricted sampling density. Distinctive morphological features of Celosieae, like multi-ovulate ovaries, are in support of the monophyly of this group (see also Fig. 4, character 4). Based on these, Cavaco (1962) even assigned subfamilial rank to the Celosieae. There is less morphological evidence for the sister group relationship of *Amaranthus* and *Chamissoa*, which is also inferred with *rbc*L (Kadereit et al., 2003) and *ndh*F sequence data (Pratt, 2003). Here we refer to the latter clade as Amaranthoids (Fig. 3b).

Subfamily Amaranthoideae is paraphyletic to the core Gomphrenoids and potentially to the traditional Gomphrenoideae depending on the first branching position and monophyly of the genus *Iresine*. The polyphyly of the tribe Amarantheae is apparent, and so is the polyphyly of Amaranthinae (Fig. 1b). In a future tribal classification system, Amarantheae will therefore have to be considerably reduced because with current sampling only *Chamissoa* groups with the nominate genus.

The likewise polyphyletic Aervinae sensu Townsend (1993) comprise two highly supported monophyletic groups, here called Achyranthoids (*Nototrichium*, *Achyranthes*, *Cyathula* Blume, *Pandiaka* Hook. f., *Sericostachys*, *Calicorema* Hook. f., *Pupalia* Juss., *Psilotrichum* Blume) and Aervoids (*Ptilotus*, *Nothosaerva* Wight, *Aerva*) (Fig. 3b). In the *rbc*L analysis, Aervoids were not resolved, with

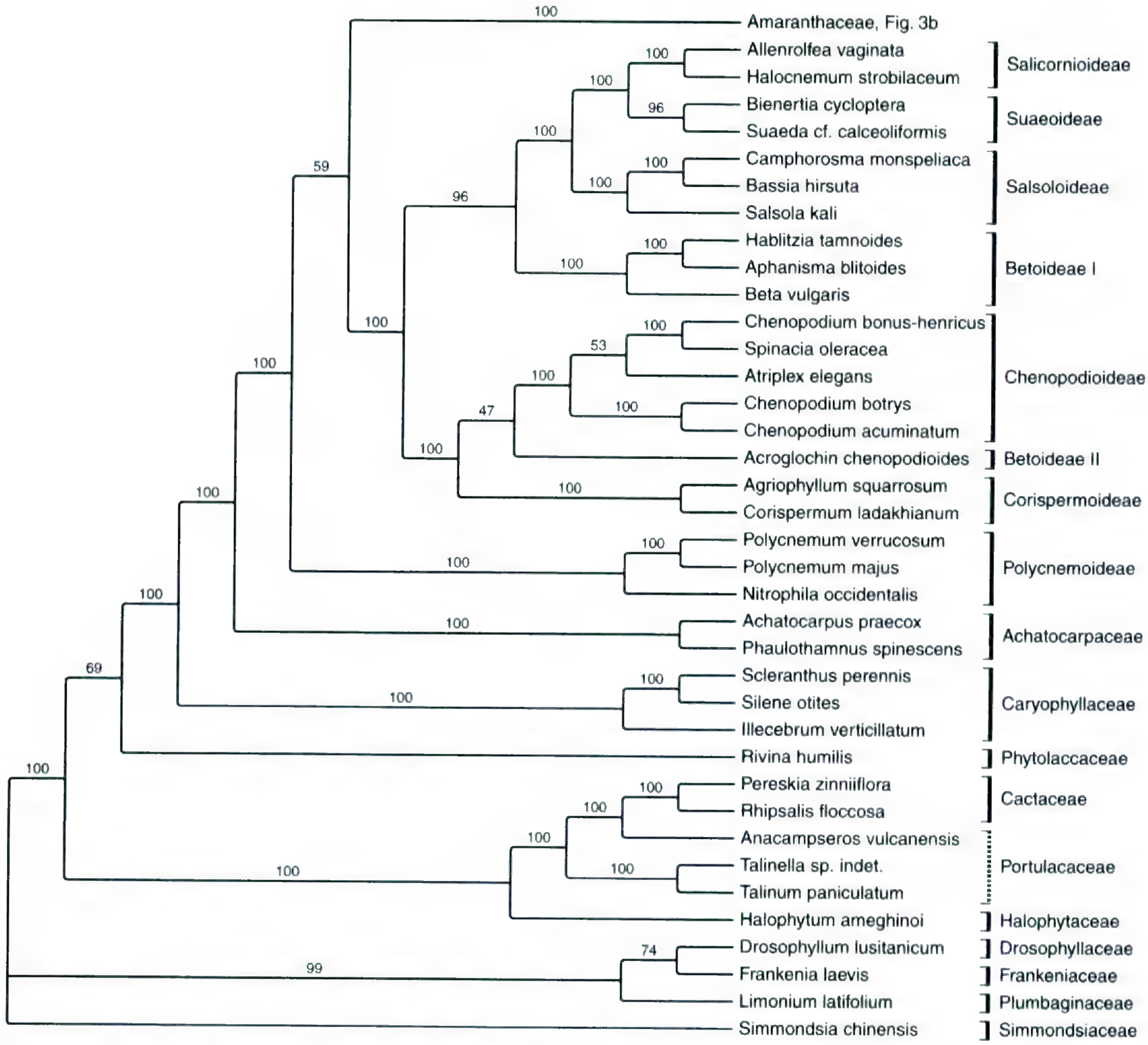


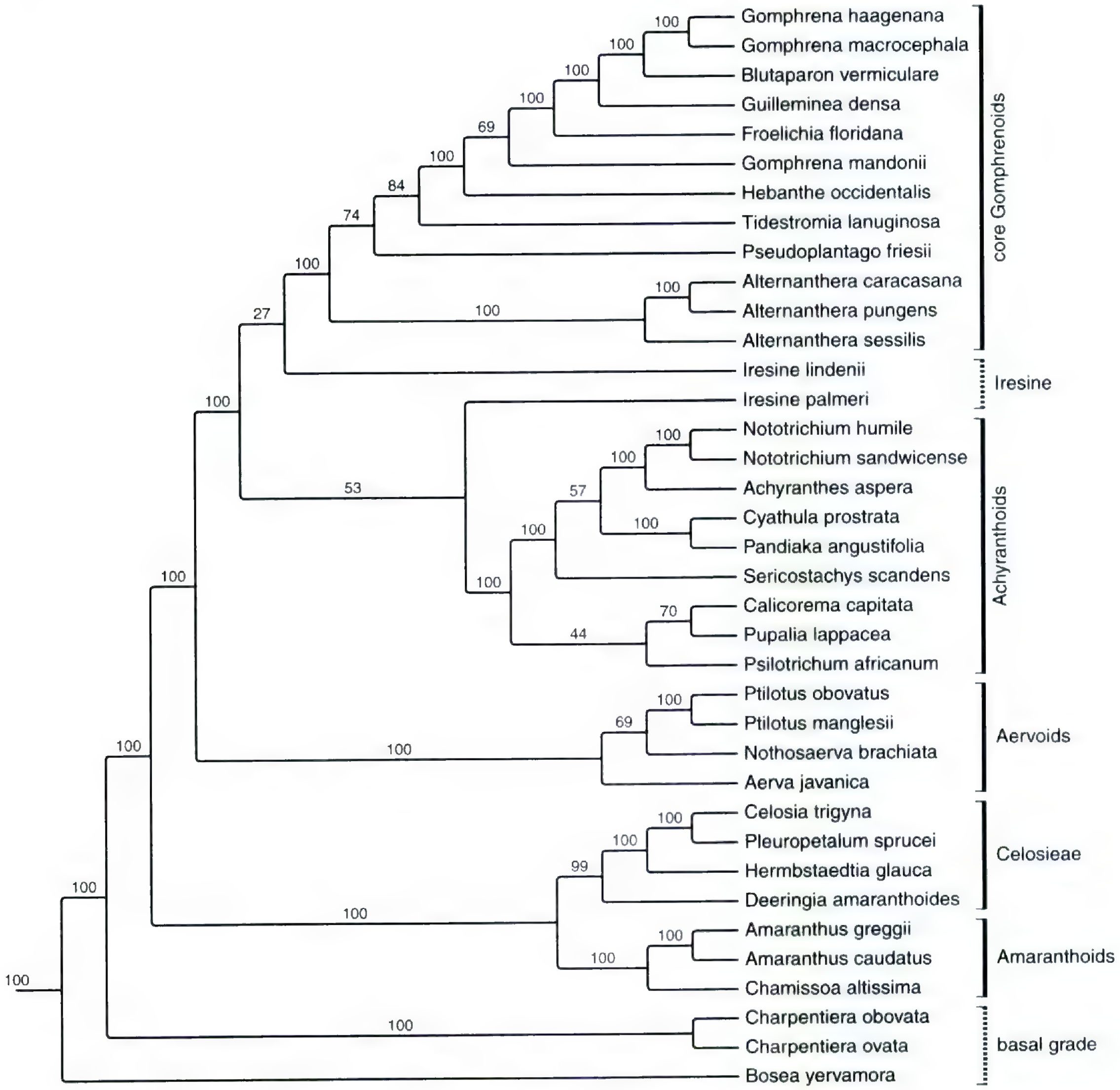
Figure 3 (pages 84–85). Consensus tree obtained from the Bayesian inference of phylogeny. Posterior clade probabilities are given above branches. Provisional taxon and clade names used in the discussion are provided right of the tree. A dashed, vertical bracket indicates apparent non-monophyly of the group to which the name refers. —a (page 84). Chenopodiaceae, closely related Caryophyllales, and outgroup. —b (page 85). Amaranthaceae.

Aerva and *Ptilotus manglesii* F. Muell. appearing in a polytomy also comprising *Iresine*, core Gomphrenoids, and Achyranthoids. Since Achyranthoids did not gain any statistical support with *rbc*L, they were provisionally called Amaranthoids II together with *Aerva* and *Ptilotus* (Kadereit et al., 2003).

Unlike the situation in the likelihood-based trees, relationships within the Achyranthoids are not entirely resolved by parsimony. In all trees, however, three highly supported clades are apparent in this group: (i) Cyathula plus Pandiaka (99% BS/100% PP; Figs. 1b/3b), (ii) Achyranthes plus Nototrichium (100% BS/PP), and (iii) the unity of (i), (ii), and Sericostachys (100% BS/PP). The achyranthoid clade harbors all species with modified sterile flowers located laterally in the cymose partial inflorescences. Otherwise, this character state only occurs in the aberrant *Pseudoplantago* of Gomphrenoideae that also has sterile flowers and bears additional traits resembling former Amaranthoideae (see Introduction and the morphological discussion below).

In the Aervoids (Fig. 3b), *Aerva* branches first, followed by *Nothosaerva* and *Ptilotus*. The two *Ptilotus* species included share many substitutions and display the highest Bremer support of all nodes (60/64 BS; Fig. 1b). They also share one of the longest deletions observed among the taxa, a 95 bp deletion (indel No. 5, see Appendix I).

With respect to the monophyly of Gomphrenoideae as previously circumscribed (Schinz, 1893, 1934; Townsend, 1993), the *trn*K data are some-



what inconclusive, leaving the position of *Iresine* unresolved under parsimony (Fig. 1b). *Iresine* is monophyletic using parsimony, which is not supported statistically, but it appears to be polyphyletic in the likelihood-based analyses (Figs. 2, 3). However, as outlined above, the conflict cannot be regarded as strong and may be explained by sampling artifacts. Similarly, the validity of 2-locular anthers as a synapomorphy for Gomphrenoideae depends on a final supported topology. Based on the current likelihood tree (Fig. 2), the assumption of a gain of 1-locular anthers in the core Gomphrenoids + Achyranthoids + Iresine clade, followed by a reversal in the Achyranthoids clade, is most parsimonious. However, it appears more probable that unilocular anthers evolved only once in a common ancestor of *Iresine* and core Gomphrenoids.

Pseudoplantago belongs to the core Gomphrenoids (defined to include all traditional Gomphrenoideae but not *Iresine*; Figs. 3b, 4). This genus is noted for its intermediate morphological set of characters, including the achyranthoid trait of having sterile flowers next to functional ones (Covas, 1939) and having 2-locular anthers like all Gomphrenoideae (cf. Fig. 4). Pollen characters of *Pseudoplantago* provide even more striking mosaics of amaranthoid and gomphrenoid character states (see Borsch, 1998). Despite this, *Pseudoplantago* was assigned to the Gomphrenoideae as tribe Pseudoplantageae (Table 1, Townsend, 1993). Molecular data not only from the present study, but also from chloroplast *rbc*L DNA sequences (Kadereit et al., 2003), support this view. Since *rbc*L does not provide convincing support and only likelihood and

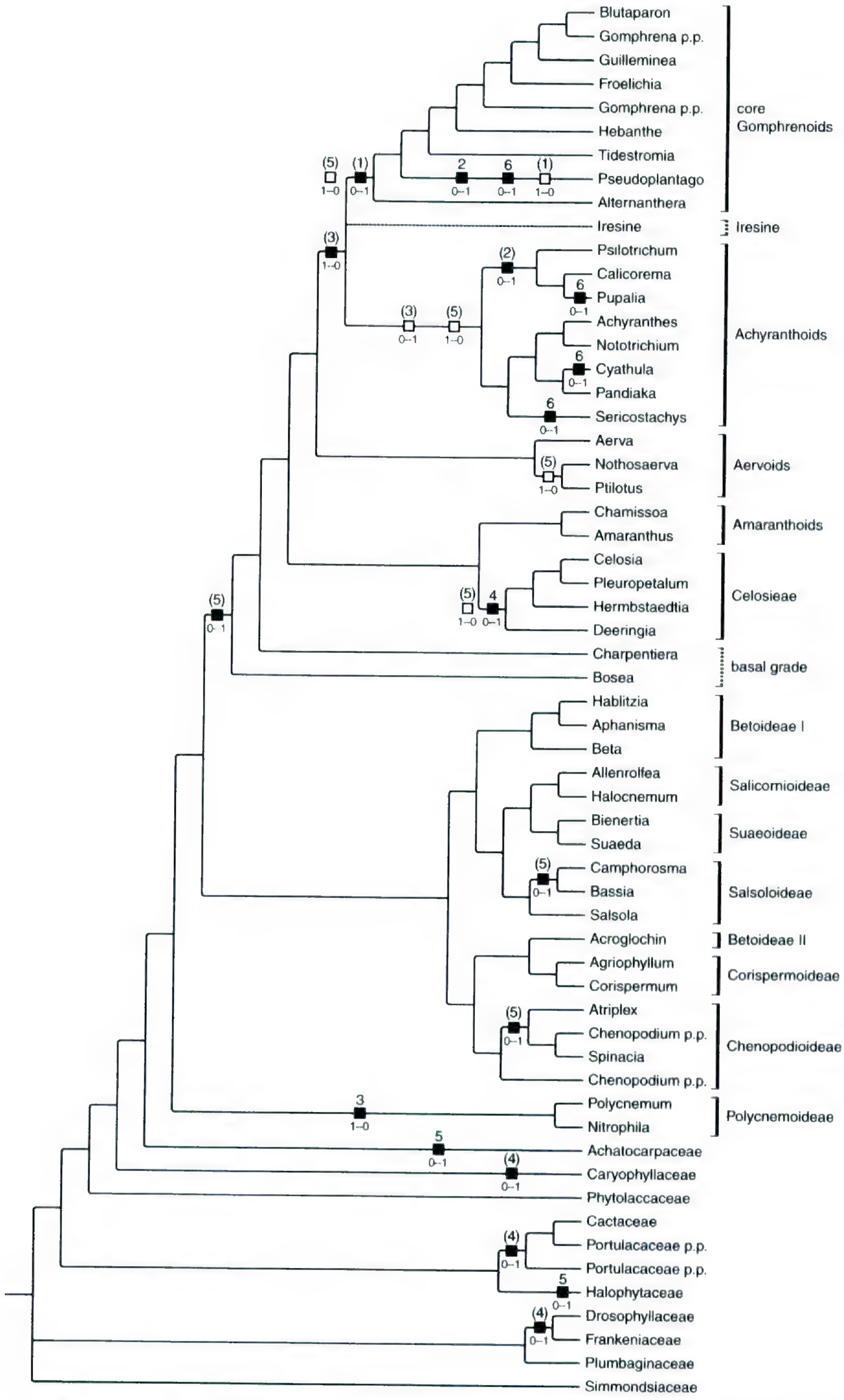


Figure 4. Simplified tree with character state transformations of selected morphological characters indicated at the branches. The tree summarizes the results of the different analyses, using clade names introduced in Figure 3. The terminals shown are reduced to genus level in the Amaranthaceae–Chenopodiaceae alliance, and to family level in the remaining Caryophyllales. A dashed, vertical bracket indicates apparent non-monophyly of the group to which the name refers. Characters were optimized using the maximum likelihood tree from Figure 2. Characters (numbers above boxes)

Bayesian inferences place some confidence on this relationship, further substantiation of the affinities of this peculiar genus will be required.

With the exception of *Pseudoplantago*, the core Gomphrenoids as defined here share metareticulate pollen (Borsch, 1998; Borsch & Barthlott, 1998). With the current sampling, *trn*K data yield too low support for the placement of *Pseudoplantago* to exclude the possibility of it branching first in this clade. Adopting this scenario, metareticulate pollen would have occurred once in the remaining core Gomphrenoids. However, the *rbc*L tree disagrees with the *trn*K tree in providing good support for a sister group relationship of *Pseudoplantago* and *Hebanthe*. Nevertheless, both genes are congruent with or at least do not strongly reject the hypothesis of a basal position of the non-metareticulate *Iresine*.

In the current circumscription of the tribe Gomphreneae (Townsend, 1993), which comprises all gomphrenoid species except *Pseudoplantago*, the subtribes Froelichiinae and Gomphreninae divide the genera into two groups. Of the genera sampled in this study, *Froelichia* Moench, *Alternanthera*, *Guilleminea* Kunth, and *Tidestromia* were classified as Froelichiinae, the remainder as Gomphreninae. *trn*K data indicate that both subtribes are polyphyletic (Fig. 1b), confirming findings based on *rbc*L data (Kadereit et al., 2003) and pollen morphology (Borsch, 1998). In core Gomphrenoids there is a grade of *Alternanthera*, *Pseudoplantago*, and *Tidestromia* as first branching taxa (Figs. 2, 3b). Good support for the nodes in the grade, however, is lacking, and a preliminary analysis of ITS and *trn*L-F sequences and morphology suggests the existence of a Tidestromia–Alternanthera clade (Sánchez-del Pino et al., unpublished data). In contrast, high support is found for a clade comprising *Hebanthe*, *Gomphrena mandonii*, *Guilleminea*, *Froelichia*, and *Blutaparon* as sister to the remaining species of *Gomphrena* (98% BS, 12/12 DC, 100% PP; Figs. 1b & 3b, respectively). *Gomphrena* had already been anticipated to be polyphyletic judging from the *Pfaffia*-type pollen occurring in the G. elegans Mart. group (here represented by *Gomphrena mandonii*, Borsch, 1998). In contrast, *Alternanthera* (represented here by three species) appears to be monophyletic (100% BS, PP; 28/32 DC), though a much denser sampling of the genus will be needed to cover more erratic representatives and increase confidence in this result. A position of *Hebanthe* distant from *Iresine* as inferred from morphological characters (Borsch & Pedersen, 1997) seems to be supported by our data.

Standley (1917) described a separate tribe Brayulineae (Table 1) based on the presence of perigynous stamens and a protruding to ascending habit with flowers solitary in the axils of cauline leaves (*Guilleminea* [formerly *Brayulinea* Small], *Tidestromia*). This was later accepted by Schinz (1934) and Cavaco (1962). Townsend (1993), however, did not uphold the separation of Brayulineae from Gomphreneae, and his view is not only supported here, but also by *rbc*L data (Kadereit et al., 2003).

RELATIONSHIPS AMONG CHENOPODIACEOUS LINEAGES

Within Chenopodiaceae, several clearly monophyletic groups are recovered here, which are largely congruent with those found in a recent analysis of *rbc*L (Kadereit et al., 2003) and *ndh*F sequences (Pratt, 2003): the Polycnemoideae, a Salicornioideae–Suaedoideae–Salsoloideae clade, the Chenopodioideae, and the Corispermoideae. A clade provisionally called Betoideae I (*Beta* L., *Hablitzia* M. Bieb., *Aphanisma* Nutt. ex Moq.) is newly recovered here, and so are the Betoideae II (consisting of the genus *Acroglochin* Schrad.), if maintained independently from Corispermoideae. Relationships among these five or six (depending on the recognition of *Acroglochin* as a distinct lineage) major chenopodiaceous lineages have been partly inconsistent between the so far recovered gene trees of *rbc*L and *ndh*F.

Major differences revealed by the *mat*K/*trn*K trees (in all analyses) as compared to previous analyses are a first branching position of Polycnemoideae in the Amaranthaceae–Chenopodiaceae alliance and a highly supported sister group relationship of Chenopodioideae and Corispermoideae plus *Acroglochin*. Although *Acroglochin* shows only weak affinities to Corispermoideae, the

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and their states (the two numbers below the boxes; the transformation direction is from the left to the right number): —1. Metareticulation of pollen grains: 0 absent, 1 present. —2. Stellate pore ornamentation of pollen grains: 0 absent, 1 present. —3. Anthers: 0 unilocular, 1 bilocular. —4. Ovule number: 0 one, 1 two to numerous. —5. Flowers on plant: 0 all hermaphrodite, 1 plants monoecious, polygamous, or dioecious. —6. Partial inflorescences of Amaranthaceae: 0 only fertile flowers, 1 modified sterile flowers present. The character state transformations with plain character numbers are unambiguous. Those with character numbers in parentheses are inferred when accelerated transitions are assumed. Open boxes represent reversals of characters that have changed in the opposite direction earlier in the tree.

confidence in the node one level deeper (cf. Fig. 1a) indicates that this genus might be quite distinct from the rest of Betoideae. Also, all Chenopodiaceae except Polycnemoideae are revealed as a monophyletic group, but with only 68% BS (but 100% PP). While *rbc*L data could not resolve the position of *Acroglochin* (Beteae), this genus is resolved away from the other Beteae with some confidence, implying the polyphyly of Beteae and Betoideae. Therefore, *Beta*, *Hablitzia*, and *Aphanisma* are provisionally identified as Betoideae I and *Acroglochin* Betoideae II.

It was observed that under parsimony the branching pattern changed significantly upon adding or removing individual taxa from Chenopodiaceae. Removing *Aphanisma*, for example, yielded an unsupported monophyletic Chenopodiaceae. Based on *rbc*L data, Polycnemoideae have been revealed as part of a trichotomy also comprising *Bosea* and the remaining Amaranthaceae (Kadereit et al., 2003), while the other subfamilies of Chenopodiaceae appear in a polytomy together with this clade. A similar result was obtained with *ndh*F sequences (Pratt, 2003). In both studies, however, support for the respective nodes is lacking or low. Polycnemoideae comprise the only genera among Amaranthaceae and Chenopodiaceae that lack anomalous secondary thickening (Carlquist, 2003) as do Achatocarpaceae. However, unlike in other chenopodioid genera, the filaments are united at the base in Polycnemoideae. Because various degrees of filament fusion are frequent in Amaranthaceae, some authors have moved *Polycnemum* and its relatives into Amaranthaceae (Endlicher, 1837; Boissier, 1879; Black, 1924; Soriano, 1944). Moquin-Tandon (1837) suggested a classification within Caryophyllaceae ("Paronychiées") based on overall similarity (growth form, shape of leaves and flowers). Identifying the phylogenetic position of Polycnemoideae will be crucial in understanding the relationship between Amaranthaceae and Chenopodiaceae. Extended character sampling currently seems to be the only way to solve this question.

With regard to betoid genera, the sister group relationship of *Hablitzia* and *Aphanisma* found with *rbc*L (Kadereit et al., 2003) is supported here, too (95% BS, Fig. 1a). The monotypic *Hablitzia* is exceptional in Chenopodiaceae in being an herbaceous liana of more or less shaded forests, whereas other genera in general are light-demanding, erect herbs or shrubs. Previously unresolved, *Beta* appears as sister to *Hablitzia* and *Aphanisma* in the *mat*K/*trn*K tree (100% BS and PP; 14 DC). A particular type of a circumscissile capsule dehiscence (yielding an operculate fruit) led Ulbrich (1934) to segregate *Beta* and *Hablitzia* together as a subfamily of their own, which was not followed by later authors. In our molecular phylogeny, the two genera do not occupy an isolated position that would justify such a division.

With the exception of *Bassia* All. and *Camphorosma* L. (Camphorosmeae), all genera of Chenopodioideae that were included in the present study constitute a well-supported clade (100% BS and PP; 15 DC; cf. Figs. 1a, 2a). This result is congruent with the *rbc*L tree (Kadereit et al., 2003), though only 54% support was obtained there, perhaps partly due to the more extensive sampling. Chenopodioideae can thus be considered monophyletic when Camphorosmeae are excluded. No conclusions can be drawn about the circumscription of Atripliceae, which are represented by only one species here.

The closely related tribe Chenopodieae, however, is inferred as paraphyletic to Atripliceae, again in correspondence with previous *rbc*L data (Kadereit et al., 2003). Presence or absence of bracteoles subtending the female flower has been most important in the morphological circumscription of both tribes. According to molecular data, this is a rather homoplastic character. In previous *rbc*L analysis (Kadereit et al., 2003), three clades of the tribe Chenopodieae have been identified and termed clades I, II, and III, and each of these three is represented here. For a more detailed discussion on the relationships within Chenopodieae, the reader is referred to Kadereit et al. (2003), who advocated a future split of this group into several tribes, partly corresponding to previously established taxa such as the Eurotinae (Volkens, 1893). Long-stalked vesicular trichomes characterize many Chenopodieae and Atripliceae. According to Carolin (1983), the occurrence of these and other unique trichome types largely agrees with the taxonomic groups as circumscribed by Scott (1977a, b) and later modified by Kühn et al. (1993).

The Corispermoideae are monophyletic (100%), confirming Kadereit et al. (2003), who in addition to our representation of the tribe sampled *Anthochlamys* Fenzl, a genus with showy tepals responsible for a somewhat Amaranthaceae-like appearance. Apart from this, the three genera are morphologically very similar, so that their union into one tribe has never been questioned. In contrast, the relationships of this subfamily to other taxa of Chenopodiaceae remain vague.

The grouping of Salsoloideae, Suaeoideae, and Salicornioideae into one clade is consistent with the previous *rbc*L analysis (Kadereit et al., 2003). The separation of Salicornioideae and Salsoloideae as

individual families (Salicorniaceae and Salsolaceae) as re-established by Scott (1977a) was not supported by the authors and again seems not warranted according to the *mat*K/*trn*K trees herein. Here both subfamilies are nested within the other chenopodiaceous lineages. Suaedoideae and Salicornioideae together formed one lineage based on *rbc*L (54% BS). The four genera (two from each subfamily) we included here form a monophyletic group (100% BS; Fig. 1a). *Bienertia* Bunge is the closest relative of *Suaeda* Forssk., thus supporting a monophyletic Suaedoideae. This corroborates the chloroplast *atp*B-*rbc*L- and *psb*B-*psb*H-spacer trees found in a study on Suaedoideae (Schütze et al., 2003), whereas *rbc*L (Kadereit et al., 2003; 75% BS) and ITS data (Schütze et al., 2003) reveal *Bienertia* as sister to Salicornioideae. Morphology is rather in favor of the first hypothesis (Kühn et al., 1993; Kadereit et al., 2003). As presently understood, there are no phenotypic characters that point toward the close affinity between the subfamilies Suaeoideae and Salicornioideae suggested by molecular data. On the other hand, a particularly close relationship between Suaedoideae and Salsoloideae, as expressed by the inclusion of Suaedeae in Salsoloideae by various authors (e.g., Kühn et al., 1993) and supported by the spirally twisted embryo in both, is neither revealed by *trn*K/*mat*K nor by *rbc*L. The *trn*K evidence instead points toward a distinct lineage Salsoloideae (100% BS/PP; 16 DC), while *Suaeda* and relatives are part of the sister clade of Salsoloideae, which also includes Salicornioideae. Both data sets are rather consistent with the view of Volkens (1893) and Ulbrich (1934), who assumed that Suaedeae and Salsoleae represent quite unrelated lineages. This hypothesis also favors the scenario of spirally twisted embryos evolving twice independently (for a more detailed discussion see Kadereit et al., 2003). The *mat*K data also support the monophyly of Salsoloideae (100% BS/PP; 16 DC; Fig. 1a), which received 88% BS with *rbc*L (Kadereit et al., 2003). The two genera (out of six) we included to represent Camphorosmeae appear in a clade supported by 100% BS/PP (Figs. 1a, 3a). In the present study, Salsoleae were represented by one species of *Salsola* only. It may be noted that Kadereit et al. (2003) found that *Salsola* L. is polyphyletic, and more detailed studies on this genus and the tribe are under way (Freitag & Kadereit, unpublished).

MORPHOLOGICAL CHARACTERS AND CLASSIFICATION OF AMARANTHACEAE

Pollen Characters

In general, pollen characters circumscribe clades within Amaranthaceae better than units of traditional systems (Table 1). As a consequence, the previously expressed hypothesis as to their utility as characters for a phylogenetic reconstruction in this group (Borsch, 1998) seems substantiated. Some individual complex pollen characters, however, appear to have been subjected to parallel evolution. This is particularly noticeable in the case of stellate pore ornamentation (Fig. 4; character 2).

The recently described metareticulate pollen (Borsch & Barthlott, 1998) differs from reticulate pollen by meshes of the reticulum that are homologous to mesoporia rather than being tectal ornamentations. Metareticulate pollen also occurs outside Amaranthaceae (e.g., in Vivianiaceae, Zygophyllaceae), while true reticulation, though previously described for Amaranthaceae (e.g., Townsend, 1993), is absent from the family. Metareticulate pollen is reconstructed as having occurred once in the ancestor of the core Gomphrenoids (Fig. 4, character 1). In *Iresine*, as well as in *Woehleria* Griseb. and *Irenella* Suess. (the latter two were not sampled here), pollen from the *Iresine*-type is found (Borsch, 1998), characterized by mesoporia that are much less vaulted than in the true metareticulate types.

With the current sampling, *trn*K data yield too low support for the placement of *Iresine* and *Pseudoplantago* to exclude the possibility of either genus being a basal lineage in the Gomphrenoideae. The *rbc*L data, however, provided good support for a sister group relationship between *Pseudoplantago* and *Hebanthe* (Kadereit et al., 2003). This pattern, though not found with *trn*K herein, leaves the possibility of a reversal of pollen and other character states in this genus. As a consequence, the hypothesis that pollen grains in *Pseudoplantago* are derived from a metareticulate architecture that is obscured by their cuboid or tetrahedral shape has to be tested.

Based on the occurrence of the metareticulate *Gomphrena* and *Pfaffia* pollen types, it has been argued that the subtribes Froelichiinae and Gomphreninae may be polyphyletic (Borsch, 1998), which has been corroborated by our study (Fig. 1b). All genera of the well-supported terminal clade (*trn*K and *rbc*L) of the core Gomphrenoids (*Gomphrena* s. str., *Blutaparon*, *Guilleminea*, and *Froelichia*) possess *Gomphrena*-type pollen, which therefore seems to be a synapomorphy of this clade.

Psilotrichopsis C. C. Towns. (Amaranthoideae–Aervinae Townsend, 1993) is also characterized by metareticulate pollen (Borsch, 1998). To assess whether metareticulation was acquired independently here, it would be of great interest to see

where the genus is placed by *trn*K or other molecular data.

Among the genera sampled, *Pseudoplantago*, *Psilotrichum*, *Calicorema*, and *Pupalia* exhibit pollen with stellate pore ornamentation (Livingstone et al., 1973; pore type IV in Borsch, 1998). In this kind of ornamentation, the pore membrane bears circularly arranged "flecks of ektexine" (Skvarla & Nowicke, 1976), here termed "ektexinous bodies" (according to Borsch, 1998), that each cover an equal segment of the pore and are distally elongated into an outwardly projecting hook. Among all angiosperms surveyed, this pore type only occurs in Amaranthaceae. Despite having stellate ornamented pores throughout, the pollen of the genera listed above has been classified to three different pollen types: *Pseudoplantago* type, *Mechowia* Schinz type, and *Psilotrichum* type (in *Psilotrichum* and *Pupalia*) (Borsch, 1998), the *Psilotrichum* type being considered least derived (Borsch, 1998). The occurrence of stellate pore ornamentation was originally understood as a synapomorphy of the genera in which it had been observed first (*Centemopsis* Schinz, *Psilotrichum*, *Pupalia*, Livingstone et al., 1973). However, its presence in additional genera (Borsch, 1998) that are obviously unrelated based on other morphological characters, indicated that this ornamentation probably evolved several times in parallel. Tracing states associated with this character (Fig. 4, character 2) supports a minimum of two independent occurrences of stellate pore ornamentation: once in the gomphrenoid *Pseudoplantago*, and a second time in the Achyranthoid clade. The situation within the latter clade is not entirely clarified, since evidence for the branching shown in Figure 4 is restricted to likelihood and Bayesian analyses, while parsimony analysis arranges genera with stellate pore ornamentation in a polytomy.

Judging from the currently available data, it appears that those genera in which stellate pore ornamentation was first described (*Centemopsis*, *Psilotrichum*, *Pupalia*, Livingstone et al., 1973, *Centemopsis* not included here) do form a monophyletic group and that in these a particular variant (the *Psilotrichum* type sensu Borsch, 1998) has a common origin (transformation under accelerated transitions of character 2 in Fig. 4). *Calicorema* and *Pupalia* constitute a clade with *Psilotrichum* as sister, but support for this is restricted to likelihood-based analyses and posterior probabilities are low (Fig. 3b). While *Pupalia* and *Psilotrichum* have pollen classified as *Psilotrichum* type, pollen of *Calicorema* was found to be heterogeneous but at least partly of the *Psilotrichum* type (Borsch, 1998). Pollen of *C. capitata* (included in the present study) belongs to the *Deeringia* type with irregularly arranged, small, unhooked ektexinous bodies. In contrast, *C. squarrosa* exhibits pollen of the typical *Psilotrichum* type. Combining this evidence, a unique origin of the *Psilotrichum* type, subsequently lost in some species of *Calicorema*, appears likely. At present, however, the fact that *Centemopsis* so far could not be included in the sampling allows no further conclusions along those lines. If monophyly of *Calicorema* is doubted and the character state of the included species *C. capitata* used instead of ambiguous coding during character tracing, a reversal in *Calicorema* has to be hypothesized under accelerated transitions and two parallel occurrences (in *Psilotrichum* and *Pupalia*) under delayed transitions.

Grains transitional to the *Centemopsis* type have been found in *Pupalia* (Borsch, 1998). Whether this is an indication of a potential common origin for the "hooks" in stellate ornamented pollen of both *Psilotrichum* and *Centemopsis* types will have to await analyses of a currently compiled *trn*K data set with increased sampling in Aervinae (Müller & Borsch, in prep.).

Pollen grains in *Pseudoplantago* also have stellate pore ornamentation, although the genus strongly deviates from other genera with stellate pore ornamentation by its tetrahedral or cubical pollen shape. Two possibilities of interpreting the occurrence of stellate pore ornamentation in *Pseudoplantago* have been discussed (Eliasson, 1988; Borsch, 1998). It could (i) hint toward a closer relationship of the genus to Amaranthoideae than previously thought (Townsend, 1993) or (ii) pending that other characters support affinities to the bisporangiate subfamily, it could mean that the rather complex set of character states evolved in parallel. Since the hypothesis of *Pseudoplantago* belonging to the traditional Gomphrenoideae (core Gomphrenoids; Fig. 3b) seems to be acceptable now, in agreement with studies using *rbc*L (Kadereit et al., 2003) and ITS1 (McCauley, 2002a, 2002b), the parallel evolution of the peculiar form and arrangement of the ektexinous bodies in this genus is apparent (Fig. 4, unambiguous transformation).

The above discussion shows that in the evolution of stellate pore ornamentation parallelisms and reversals are much more likely than in metareticulate pollen types. One rationale could be that stellate pore ornamentation somehow plays a role in insect pollination, so that it was selected for in independent lineages (Livingstone, 1972).

Other Morphological Characters

Among the characters traditionally used in classification, anther locule number and ovule number

have been exemplarily examined in a phylogenetic framework using the results of the present study. The differences in anther locule number have led to the separation of Amaranthoideae and Gomphrenoideae or equivalent taxa found in most systems (Table 1). On the likelihood tree (Fig. 2), the locule number of anthers is reconstructed as having changed from two to one at the node uniting Gomphrenoids, *Iresine*, and Achyranthoids (Fig. 4, character 3), followed by a reversal back to the two-locular state in the Achyranthoids. Due to the remaining questions regarding *Iresine* that were outlined above, this hypothesis needs further testing. Consequently, the presumed synapomorphy and diagnostic character for Gomphrenoideae of 2-locular anthers has to remain uncontradicted for the time being.

Ovaries are unambiguously reconstructed to have changed to a multi-ovulate state in the ancestor of Celosieae (Fig. 4, character 4). Outside Amaranthaceae, however, this character is highly homoplastic, having changed several times in parallel from uni- to pluriovulate (Fig. 4; character 4 in brackets; state transformations found reconstructed assuming accelerated transition). Based on pluriovulate ovaries, Cavaco (1962) even assigned subfamilial rank to the Celosieae (Table 1).

On the branch leading to Amaranthaceae, a transformation from plants with exclusively bisexual flowers (monoclinous breeding system) to plants with unisexual flowers (diclinous breeding system; monoecious, polygamous, or dioecious plants) is reconstructed (Fig. 4, character 5). The first branching genera, *Bosea* and *Charpentiera*, both have functionally unisexual flowers. This state is later reversed several times independently according to an optimization scheme that assumes accelerated transitions. However, the exact localization and number of transformations of this character heavily depend on further elucidation of the branching order at the base of the Amaranthaceae tree that is currently in conflict with *ndh*F data (Pratt, 2003) and on inclusion of additional genera of the Aervinae. Similarly, Achatocarpaceae and several clades within Chenopodiaceae appear to have acquired a diclinous breeding system in parallel.

Altogether four independent gains of a type of partial inflorescence architecture that includes modified sterile flowers subtending a central fertile flower are reconstructed (Fig. 4, character 6). While the independence of the gain in *Pseudoplantago* is assured, the three gains traced in the Achyranthoids again depend on a topology that is not entirely certain. This is the case because only likelihood-based approaches infer the branching pattern as illustrated in Figure 4, whereas parsimony does not completely resolve this part of the tree.

Conclusion

The surprising composition of a basal grade within Amaranthaceae is substantiated, having considerable consequences for biogeography and character evolution. Two new major clades are recognized, which are the exclusively palaeotropical Aervoids and the Achyranthoids, which are palaeotropical with an extension onto the Pacific islands. These findings underscore that a further increase in taxon sampling is needed, in particular as hardly any predictions can be made with respect to other Amaranthoideae that might belong to the basal grade. For this reason, the clade names suggested in this paper are not yet nomenclaturally formalized. Previous studies with a more extensive sampling agree with this study on the non-monophyly of Chenopodiaceae as currently classified, though without convincing support. However, whether two monophyletic families, Chenopodiaceae and Amaranthaceae, can be maintained by either shifting Polycnemoideae to Amaranthaceae or treating them as independent families, needs further study.

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Appendix I. List of indels found in the *trn*K intron. The position in the alignment and the extension of each indel are noted (bp). SSR = simple sequence repeat. When sequence motifs are provided, the IUPAC ambiguity code is followed.

*trn*K-Intron 5′ part

1. "ATAT" double SSR from "AT" ranging in bp 39–44.
2. "CTGAA" SRR ranging at bp 77–86.
3. Probably deletion of A at bp 90.
4. Indel, probably deletion at bp 120–129 (10 bp).
5. Indel, probably deletion at bp 123–258 (probably 95 bp deletion).
6. Indel, probably deletion at bp 142–143 (2 bp).
7. Indel, probably deletion at bp 144–147 (4 bp).
8. Indel, probably insertion of unknown origin, bp 151–155 ("AAATT").
9. Indel, probably deletion at bp 157–173 (probably 12 bp).
10. "CAAAT" SSR ranging at bp 157–166.
11. Indel, probably deletion at bp 167–178 (probably 11 bp).
12. Indel, probably deletion at bp 169–179 (probably 10 bp).
13. "A" SSR ranging from bp 174–175.
14. "CTATK" SSR with 1 substitution ranging from bp 180–193.
15. "AACA" SSR ranging at bp 176–188.
16. "T" SSR ranging at bp 194–195.
17. "G" SSR ranging at bp 196–197.
18. Indel, probably deletion at bp 200 (1 bp).
19. Indel, probably deletion at bp 197–223 (probably 14 bp).
20. Indel, probably deletion at bp 200–208 (probably 3 bp).
21. "CATTTC" indel, insertion of unknown origin in bp 202–207.
22. Indel, probably deletion at bp 208–223 (probably 9 bp).
23. "GGCTTTT" indel, probably insertion of uncertain origin at bp 211–217.
24. Indel, probably deletion in bp 220–230 (probably 11 bp).
25. Indel, probably deletion at bp 220–224 (probably 5 bp).
26. Indel, probably deletion at bp 227–228 (2 bp).
27. Indel, probably deletion at bp 229 (1 bp).
28. "AAAGC" SSR that may have been partially lost or was partially repeated at some taxa (multiside indel). 1 = AAAGC in *Amaranthus caudatus*, *A. greggii*, *Chamissoa altissima*; 2 "AAA" in *Hablitzia tamnoides*; and 3 = "A" in *Celosia trigyna*.
29. "A" or "G" insertion of unknown origin at bp 244.
30. Indel, probably deletion at bp 245 (1 bp).
31. "A" SSR ranging from bp 280–281.
32. "GGT" SSR ranging from bp 283–295.
33. Insertion of unknown origin that may have been partially lost or was partially repeated in some taxa (multistate indel) ranging from bp 286–292.
34. Indel, probably deletion at bp 308 (1 bp).
35. Indel, probably deletion at bp 312 (1 bp).
36. "TAAAGAA" insertion of unknown origin, bp 313–319.
37. "AAAA" SSR that may have been partially lost or partially repeated in some taxa (multistate indel) ranging from bp 320–327.

Appendix I. Continued.

38. "A" insertion of unknown origin at bp 343.
39. "TSAAK" SSR ranging from bp 353–362.
40. "GATCTAA" SSR ranging from bp 371–384.
41. Indel, probably deletion at bp 428 (1 bp).
42. Indel, probably deletion at bp 428 (1 bp).
43. Indel, probably deletion at bp 431 (1 bp).
44. Indel, probably deletion at bp 453 (1 bp).
45. "A" insertion of unknown origin at bp 454.
46. "A" SSR ranging from bp 463–464 (1 bp).
47. Indel of 2 bp at bp 464–465.
48. Indel, probably deletion ranging from bp 483–489 (5 bp).
49. "AC" insertion of unknown origin at bp 486–487.
50. "AATCTTTA" SSR ranging from bp 494–514.
51. Indel, probably deletion at bp 503–507 (5 bp).
52. "MATAA" SSR ranging from bp 508–519.
53. "A" series that has probably been duplicated or lost (not highly variable and thus not considered a microsatellite but a multistate) ranging from bp 515–517. 0 = "T," 1 = "TT," 2 = "TTT."
54. Large indel, probably deletion from bp 515 (or bp 517) to bp 535.
55. Indel, probably deletion at bp 518–535 (probably 6 bp).
56. "TTAAGAG" SSR ranging from bp 516–534.
57. "TAAGG" SSR ranging from bp 517–533.
58. "GATGAA" SSR with several substitutions ranging from bp 541–552.
59. Indel, probably deletion at bp 776–777 (2 bp).
60. "AAA" Indel of unknown origin, bp 779–781.
61. "AGAAT" SSR ranging from bp 776–788.
62. Indel, probably deletion at bp 804 (1 bp).
63. Indel, probably deletion at bp 806–813 (probably 7 bp).
64. "A" indel of unknown origin, bp 810.
65. Indel, probably deletion at bp 818 (1 bp).
66. Indel, probably deletion at bp 823 (1 bp).
67. "A" indel of unknown origin, bp 824.
68. Indel, probably deletion at bp 825–830 (probably 6 bp).
69. "CTCATCTCTATTAGTT" insertion of probably complex SSR-origin at bp 831–846; parts are a repeat structure that must have been partly repeated a second time.
70. "TTTATTT" SSR ranging from bp 823–853. Can be explained as SSR if insertion of character 67 is considered to have happened at a later time.
71. "TWTTT" SSR ranging from bp 826–858.
72. "ATTATTCGAATATAAAATTATTAGAAAT" insertion of probably complex SSR, origin at bp 859–886.
73. "AA" SSR ranging at bp 885–888.
74. Indel, probably deletion at bp 887 (1 bp).
75. Indel, probably deletion at bp 888–889 (1 bp).
76. Indel, probably deletion at bp 890 (1 bp).
77. Indel, "ARAATA" SSR at bp 893–894.
78. Indel, probably deletion at bp 898 (1 bp).
79. "A" SSR, motif ranging at bp 908–909.
80. Indel, probably deletion at bp 921 (1 bp).
81. "A" indel of unknown origin, bp 931.
82. Indel, probably deletion at bp 957 (1 bp).
83. Indel, probably deletion at bp 958–961 (4 bp).
84. Indel, probably deletion at bp 961 (1 bp).
85. "TATATATATA" microsatellite, insertions ranging from bp 962–971 (1 = Sericostachys), may be reduced by multiple mutations to "A" at bp 971 (2 = *Hablitzia*).
86. Indel, probably deletion at bp 1025–1027 (3 bp).
87. Indel, probably deletion at bp 1025–1026 (2 bp).
88. Indel, probably deletion at bp 1026–1029 (4 bp).
89. Indel, probably deletion at bp 1030–1036 (6 bp).
90. Indel, probably deletion at bp 1030 (1 bp).
91. "G" SSR, motif ranging from bp 1032–1033.
92. Indel, probably deletion at bp 1029–1036 (7 bp).
93. Indel, probably deletion at bp 1031–1036 (5 bp).
94. "AAATT" SSR, motif from bp 1037–1046.

A highly variable microsatellite from bp 1050 to bp 1066 is not excluded because there are no mutations, but it is also not coded since no information exists about infraspecific variability.

Appendix I. Continued.

95. "ATGSWAA" SSR motif from bp 1067–1086, it may be a copy from the start of the gene, which is considered to be part of the spacer since the indel is not a multiple of three; a state that is only 5 bp also appears. 1 = *Rivina humilis*, 2 = *Frankenia laevis*, *Simmondsia chinensis*.

*mat*K-CDS

96. "ATSRAM" SSR, motif extending from bp 1074–1085 (1–12 of CDS). Is considered to be part of the gene, since otherwise there would be no stop codon.
97. "YGATTT" SSR, motif extending from bp 1084–1095 (105–116 of CDS).
98. Indel, probably deletion from bp 1197–1205 (between bp 111 and bp 112 of CDS).
99. "TTA" indel, may be deletion at core Caryophyllales from bp 1226–1228.
100. Indel, probably deletion from bp 1300–1302 (between 220 and 221 of CDS).
101. Indel, probably deletion from bp 1317–1325 (between bp 228 and bp 229 of CDS).
102. Indel, unclear whether deletion from bp 1347–1352.
103. Indel, probably deletion from bp 1412–1417. The two codons are deleted irrespective of reading frame.
104. Indel, probably deletion from bp 1416–1424.
105. Indel, probably deletion from bp 1422–1427.
106. Indel, probably deletion from bp 1428–1436.
107. "GAAAAAGAA" SSR, motif from bp 1437–1460.
108. "GYAAAA" SSR, motif from bp 1446–1457.
109. Indel, probably deletion from bp 1458–1460.
110. "AAAGAA" SSR, motif from bp 1455–1466.
111. "AAGCAA" SSR, probably insertion of unknown origin at bp 1467–1472.
112. "AAACGT" SSR, probably insertion of unknown origin at bp 1473–1478.
113. "AAT" double-SSR, motif from bp 1680–1685.
114. Indel, probably deletion from bp 1713–1721.
115. "AAAGTT" SSR with different substitutions, motif from bp 1893–1904.
116. "TTTACT" SSR, motif from bp 1905–1916.
117. Indel, probably deletion from bp 1911–1916.
118. "TCT" SSR, motif from bp 2015–2020.
119. Indel, probably deletion from bp 2577–2585.
120. Indel, probably deletion from bp 2589–2591.
121. "TATATA" SSR, probably satellite that arose from more than one insertion, motif from bp 2598–2607.
122. "ATTCATAAT" SSR, motif from bp 2640–2657.
123. "TTAGTY" SSR, motif from bp 2658–2669.

*trn*K-intron 3′ part

124. "AMTGATC" SSR, motif from bp 2670–2684.
125. "A" SSR, motif from bp 2679–2680.
126. "ACTGATC" SSR, motif from bp 2677–2691.
127. "AATGA" SSR, motif from bp 2692–2722.
128. "AATTGATATT" indel, probably insertion in *Limonium*, bp 2700–2709.
129. "GMTTTTGATTM" SSR motif from bp 2710–2736.
130. "TT" SSR, motif from bp 2723–2726.
131. "ATTGK" SSR, motif from bp 2722–2733.
132. Indel, probably deletion from bp 2734–2737.
133. "TTTTGTTATAAG" SSR, motif from bp 2724–2767.
134. "GATTA(G)T" SSR, motif from bp 2727–2756.
135. "TTGGTTAT" SSR, motif from bp 2726–2764.
136. "AAATGGAATGGAAATTATACCT" indel from bp 2775–2796.
137. "AAGCT" indel, of unknown origin from bp 2797–2801.
138. "AATAT" indel, of unknown origin from bp 2802–2806.
139. "AACTAACGGAAAACT" indel, of unknown origin from bp 2807–2821.
140. Indel, probably deletion from bp 2822–2824.
141. "ATYTAAAT" SSR, motif from bp 2771–2833.
142. Indel, probably deletion from bp 2822–2857 (probably 29 bp).
143. Indel, probably deletion at bp 2834 (probably 1 bp).
144. Indel, probably deletion at bp 2837 (probably 1 bp).
145. Indel, probably deletion from bp 2837–2865 (probably 21 to 22 bp).
146. Indel, probably deletion at bp 2840 (probably 1 bp).
147. "T" SSR, motif from bp 2840–2841.
148. "AYCTA" SSR, motif from bp 2849–2858.
149. "T" indel, of unknown origin at bp 2859.
150. Indel, probably deletion from bp 2860–2863 (probably 4 bp).
151. Indel, probably deletion from bp 2843–2870 (probably 21 bp).

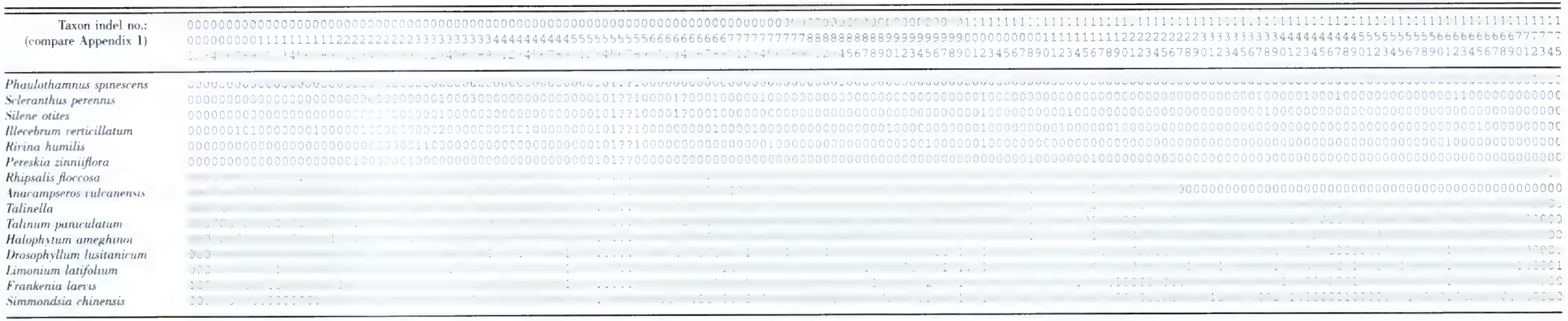
Appendix I. Continued.

152. Indel, probably deletion from bp 2865–2873 (probably 8 bp).
153. "A" SSR, motif from bp 2869–2870.
154. Indel, probably deletion from bp 2868–2871 (probably 3 bp).
155. Indel, probably deletion from bp 2870–2873 (probably 4 bp).
156. Indel, probably deletion from bp 2902–2904 (probably 3 bp).
157. Indel, probably deletion from bp 2913–2916 (probably 4 bp).
158. "CTGAAA" SSR, motif from bp 2918–2929.
159. Indel, probably deletion from bp 2934–2944 (probably 5 bp).
160. Indel, probably deletion from bp 2935–2945 (probably 5 bp).
161. Indel, probably deletion from bp 2943–2949 (probably 6 bp).
162. "A" SSR, motif from bp 2947–2948.
163. "GCAATTT" SSR, motif from bp 2950–2956.
164. "MAAT" SSR, motif from bp 2958–2965.
165. "ATGCTTATACAAWAAAT" SSR, motif from bp 2935–2986.
166. "TKCAAT" SSR, motif from bp 2949–2969.
167. "AATAGG" SSR, motif from bp 2959–3016.
168. Indel, probably deletion from bp 3021–3028 (probably 8 bp).
169. Indel, probably deletion from bp 3040 (probably 1 bp).
170. Indel, probably deletion from bp 3035–3056 (probably 10 bp).
171. "TGAGTATTCAAC" SSR, motif from bp 3029–3052.
172. "YT" SSR, motif from bp 3063–3066.
173. "TTTGTT" indel, of unknown origin at bp 3109–3114.
174. Indel, probably deletion from bp 3117–3119 (probably 2 to 3 bp).
175. Indel, probably deletion from bp 3122–3125 (probably 4 bp).

Appendix II. Indel character states for all taxa. For a description of indel characters, see Appendix 1.

Taxon indel no.: (compare Appendix 1)	0000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000000001111111111111111111111111111111111111111111111111111 / 0000000001111111111222222222233333333334444444444555555555566666666667777777777888888888899999999990000000000111111111122222222223333[illegible]44444444[illegible] / [illegible]
Alternanthera caracasana	[illegible] 000000100000100000000000000001????0000000000000001000000001000
Alternanthera pungens	00000000000010000100000000000000000010000000000100000000000000000000000000000000000000000000000000000000000100000010000 [illegible]
Alternanthera sessilis	0000000000000000000000000000000000000000010000000000000000000000000000000000000000000000000000000000100000100001101000100000000000001????0000000000001100000000100
Tidestromia lanuginosa	00000000000000000000000000000000000000001000002000100000000000000000000000000000000000[illegible]1????[illegible]
Blutaparon vermiculare	000000000000000000000000000000000000000010000000000000000000000000000000000000000001?000000000000000010000010000000000001000000000000001????0000000000000000000000000
Froelichia floridana	00000000000000000000000000000000000000001000000000000000000000000000000000000000000010000000000000000100000100000000000100000000000001????00000000000000000000000000
Gomphrena haagenana	[illegible]
Gomphrena mandonii	0000000000000000000000000000000000000000100000000000000000000000000000000000000000000000000000000000010000001000010000 [illegible]
Aerva javanica	000000000000000000000000000000000000000010000000000000000000000000000000000000000000000000000000000100000010000001100[illegible]01????000000000000000000000000000
Gomphrena macrocephala	00000000000000000000000000000000000000001100000000000000000000000000000000000000000000000001000000 [illegible] 000001000000100000000000100000000000001????0000000000000000000000000
Guilleminea densa	0000000000000000000000 [illegible]
Iresine palmeri	[illegible]
Iresine lindeni	[illegible]
Nothosaerva brachiata	00000000000000000000000000000000000000001000000000000000000000000000000000000000000000000000000000 [illegible]
Calicorema capitata	0000000000000000000000000000000000000000100000000000000000000000000000000000000000000000000000000 [illegible] ????000000000000000000000000000
Chamissoa altissima	000000000000000000000000001000000000000000000010000000000000000000100000 [illegible] ???00000000000000000000000010
Amaranthus greggii	[illegible] ????000000000000000000000000000
Amaranthus caudatus	0000000000000000000000000001000000000000000000 [illegible]
Bosea yervamora	0000000000000000000000000000000000000000100000000000000000000000000000000000000000000000000000000000000001010000000000010000010000000001?..??0000000000000000000000000
Celosia trigyna	0000000000000000000000000030000000000000000000100000000000000000000000000000001000000000000000000000001000000000001010000000000010010010000000001????0000000000000000000000020
Charpentiera obovata	0000000000000000000000000000000000000000100000000000000000000000000000000000001000000000000000000000000000000000001010000000000010000110000000001????0000000000000000000000000
Charpentiera ovata	00000000000000000000000000000[illegible]000000000000000000000000000000000000000000000000000000000000000000001010000000000010000110000000001????0000000000000000000000000
Hermbstaedtia glauca	[illegible] 0000000000000000000000000000000000010000000000000000 [illegible] 1????0000000000000000000000000
Pleuropetalum sprucei	0000000000000000000000000000000000000000100000000000000000000000000000000000000000000000000000000000000000000001010000000000010000000000000001????0000000000000000000000000
Deeringia amaranthoides	0000000000000000000000000000000000000000100000000000000000000000000000000000000000000000000000000000000000000001010000000000010000000000000001????0000000000000000000000000
Achyranthes aspera	0000000000000000000000000000000000000000100000000000000000000000000000000000000000000000000000000000000000000001000000000000100000000000000001????0000000000000000000000000
Nototrichium humile	[illegible] 000000000010 [illegible] 0000000000000000000000000000000000000000000000000000100000000000100000000000001????[illegible]
Nototrichium sandwicense	[illegible]
Cyathula prostrata	[illegible]
Pandiaka angustifolia	[illegible]
Sericostachys scandens	[illegible]
Pseudoplantago friesii	[illegible]
Hebanthe occidentalis	[illegible]
Psilotrichum africanum	[illegible]
Ptilotus obovatus	[illegible]
Ptilotus manglesii	[illegible]
Pupalia lappacea	[illegible]
Hablitzia tamnoides	[illegible]
Acroglochin chenopodioides	[illegible]
Agriophyllum squarrosum	[illegible]
Allenrolfea vaginata	[illegible]
Camphorosma monspeliaca	[illegible]
Atriplex elegans	[illegible]
Bassia hirsuta	[illegible]
Beta vulgaris	[illegible] 00000000000000000000000000000000000000000000000000000000000000000000000000010000000000100000000000000000000000
Bienertia cycloptera	0000000000000000000000000000000001000000000000001000001000000000000000000000000000000000000000000000000000000000000000000000000000000010000000000000000000000000000
Chenopodium bonus-henricus	0000000000000000000000000000000100000000000100000100000000000000000000000000000000000000001000000000000000000000000000000000000000000100000000000000000000000000
Chenopodium botrys	000000000000000000000000000000000000000000001000000000000000000000000000000001?000000000000000000000000010000000000000000000000000000000000000001000000000100000000000000
Chenopodium acuminatum	0000000000001000000000000000000000000000000001000000000100000000000000000000000000001?0000000000000000000000000000000000000000000000000000000000000000000001000000000000000
Corispermum ladakhianum	[illegible]
Polycnemum verrucosum	[illegible]
Polycnemum majus	[illegible]
Nitrophila occidentalis	[illegible]
Spinacia oleracea	[illegible]
Suaeda cf. *calceoliformis*	[illegible]
Halocnemum strobilaceum	[illegible]
Salsola kali GC	[illegible]
Aphanisma blitoides	[illegible] 0000000000000000000000000000000000000000000000000000000000000000000000000000000000000000001000000000000000000000000
Achatocarpus praecox	00000000000000000000000000000000000000000000000101??1000000000000000000000000000000001000000000000000000000000000000000000000000000000000000000000000000000000000000000

Appendix II. Continued.



Appendix III. Morphological matrix. Characters and their states are: 1 metareticulation of pollen grains: 0 absent, 1 present; 2 stellate pore ornamentation of pollen grains: 0 absent, 1 present; 3 anthers: 0 unilocular, 1 bilocular; 4 ovule number: 0 one, 1 two to numerous; 5 flowers on plant: 0 all hermaphrodite, 1 plants monoecious, polygamous, or dioecious; 6 partial inflorescences of Amaranthaceae: 0 only fertile flowers, 1 morphologically modified sterile flowers present. If more than one state occures, brackets unite them.

Taxon	Character no.: 123456
Aerva javanica	001012
Alternanthera caracasana	100002
Alternanthera pungens	100002
Alternanthera sessilis	100002
Tidestromia lanuginosa	100002
Blutaparon vermiculare	100002
Froelichia floridana	100002
Gomphrena haagenana	100002
Gomphrena mandonii	100002
Gomphrena macrocephala	100002
Guilleminea densa	100002
Iresine palmeri	000012
Iresine lindenii	000012
Nothosaerva brachiata	001002
Calicorema capitata	001002
Chamissoa altissima	0010[01]0
Amaranthus greggii	001010
Amaranthus caudatus	001010
Bosea yervamora	0010[01]0
Celosia trigyna	001100
Charpentiera obovata	001012
Charpentiera ovata	001012
Deeringia amaranthoides	0011[01]2
Pleuropetalum sprucei	001102
Hermbstaedtia glauca	001100
Achyranthes aspera	001002
Nototrichium humile	001002
Nototrichium sandwicense	001002
Cyathula prostrata	001001
Pandiaka angustifolia	001000
Sericostachys scandens	001001
Pseudoplantago friesii	010001
Hebanthe occidentalis	100000
Psilotrichum africanum	011000
Ptilotus obovatus	001000
Ptilotus manglesii	001000
Pupalia lappacea	011001
Hablitzia tamnoides	00100-
Acroglochin chenopodioides	00100-
Agriophyllum squarrosum	00100-
Allenrolfea vaginata	00100-
Camphorosma monspeliaca	0010[01]-
Atriplex elegans	00101-
Bassia hirsuta	00101-
Beta vulgaris	00100-
Bienertia cycloptera	0010[01]-
Chenopodium bonus-henricus	0010[01]-
Chenopodium botrys	0010[01]-
Chenopodium acuminatum	0010[01]-
Corispermum ladakhianum	00100-
Polycnemum verrucosum	00000-
Polycnemum majus	00000-
Nitrophila occidentalis	00000-
Spinacia oleracea	00101-
Suaeda cf. *calceoliformis*	0010[01]-
Halocnemum strobilaceum	00100-
Salsola kali	00100-
Aphanisma blitoides	00100-
Achatocarpus praecox	00101-
Phaulothamnus spinescens	00101-
Scleranthus perennis	00110-
Silene otites	00110-
Illecebrum verticillatum	00110-
Rivina humilis	00100-
Pereskia zinniiflora	00110-
Rhipsalis floccosa	00110-
Anacampseros vulcanensis	001[01]0-
Talinella	001[01]0-
Talinum paniculatum	001[01]0-
Halophytum ameghinoi	00101-
Drosophyllum lusitanicum	00110-
Limonium latifolium	00100-
Frankenia laevis	00110-
Simmondsia chinensis	00111-

RESURRECTION AND REVISION OF *PATIMA* (RUBIACEAE, CINCHONOIDEAE, HAMELIEAE)[1]

Piero G. Delprete,[2,3,4] *Michael Nee,*[5] *and Jifke Koek-Noorman*[2]

ABSTRACT

Because of its complex taxonomic history, the identity, circumscription, and systematic position of *Patima* (Rubiaceae) have been nebulous. After a careful morphological analysis, *Patima* is here recognized as a monospecific genus endemic to the eastern portion of the Guayana Shield. Two names in Rubiaceae are here treated as new synonyms with *Patima guianensis* Aubl., *Patima formicaria* I. M. Johnst. and *Hoffmannia megistophylla* Standl. Two names described under *Patima*, *P. laxiflora* Benth. (here lectotypified) and *P. forsythii* DC., are shown to belong to other Rubiaceae genera. *Aegiphila gleasonii* Moldenke (described as a taxon in the Verbenaceae) is another new synonym of *Patima guianensis*. *Patima* is here included in the tribe Hamelieae (subfamily Cinchonoideae) because of its morphological features and its overall similarity to *Hoffmannia*. The presence of raphides in *Patima* (declared to be absent by previous authors) is here confirmed and discussed. A full account of the taxonomic history and systematic position of *Patima*, complete typification, complete generic and specific descriptions, a distribution map, a line drawing, photographs of raphides, and observations on ant/plant interaction are provided.

Key words: *Aegiphila*, Brazil, French Guiana, Guyana, Guayana Shield, Hamelieae, *Hoffmannia*, *Kutchubaea*, *Patima*, *Retiniphyllum*, Rubiaceae, South America, Verbenaceae.

The genus *Patima* Aubl. was described by Aublet (1775) from a plant collected in French Guiana during his stay there from 1762 to 1764. The generic name is derived from *Patima-rana*, the Carib name reported by Aublet. The systematic position, generic delimitation, and the number of species ascribed to *Patima* became increasingly confused over the next two centuries, as can be seen in the taxonomic history below. The single species here recognized was listed in the *Checklist of the Plants of the Guianas (Guyana, Surinam, French Guiana)* (Boggan et al., 1997) under three different genera in two different families, as *Patima guianensis* Aubl. (Rubiaceae), *Hoffmannia megistophylla* Standl. (Rubiaceae), and *Aegiphila gleasonii* Moldenke (Verbenaceae). On the other hand, two other species described under *Patima* belong to other Rubiaceae genera instead: *Patima forsythii* DC. does not belong to this genus and is a taxon of dubious identity, and *Patima laxiflora* Benth., here typified, is confirmed to be a species of *Retiniphyllum* Bonpl. We give here an account of its complex taxonomic history and systematic placement, and the presence of raphides is here discussed and illustrated for the first time. In addition, complete generic and specific descriptions, distribution map, line drawing, and observations on ant interactions are presented.

MATERIAL AND METHODS

The present revision is based on the examination of herbarium specimens and field observations conducted in French Guiana, in 1999, with the assis-

[1] We are grateful to the directors and curators of BR, CAY, GH, MO, NY, U, and US for making their collections available for this study, to Muriel Hecquet (G) and Fernand Jacquemoud (G) for sending images of the type of *Patima forsythii* from the Prodromus Herbarium (G-DC), to Steve Cafferty (BM) for sending images and additional information about the type of *Patima guianensis*, to Tom Wendt (LL/TEX) for checking about possible information in the Moldenke Herbarium housed in his institution, and Dewanand Makhan (U) for the skillful assistance with the preparation of the anatomical slides and the search for raphides in *Patima guianensis*. Finally, we wish to express our gratitude to Elmar Robbrecht (BR) and an anonymous reviewer for helpful comments to the manuscript and for encouraging a more extensive search for raphides.

[2] National Herbarium of the Netherlands, Utrecht University Branch, Plant Systematics, Heidelberglaan 2, 3584 DV Utrecht, The Netherlands.

[3] Current address: Federal University of Goiás, Campus II, Institute of Biological Sciences, Department of General Biology, ICB-1, 74001-970 Goiânia, Goiás, Brazil.

[4] Author for correspondence: pdelprete@hotmail.com.

[5] Institute of Systematic Botany, The New York Botanical Garden, Bronx, New York 10458-5126, U.S.A.

tance of Françoise Crozier (CAY). Approximately 50 specimens from BR, CAY, GH, MO, NY, U, and US were studied and annotated (see specimens cited). Digital images of the type specimens of *Patima forsythii* DC. preserved at the Prodromus Herbarium (G-DC) were analyzed and printed (copies were deposited at NY).

Material used for anatomical studies was extracted from herbarium specimens. Voucher specimens are preserved at the National Herbarium of the Netherlands, Utrecht University Branch (U), and the wood voucher at the Wood Collection (Uw) of the same institution. The following specimens were studied (see specimens cited for collection localities): *Henkel et al. 4941*, flowers and young fruits; *Granville & Crozier 5829*, flower buds, bark and wood (Uw 29792); *Granville & Crozier 13650*, flower buds and leaves; *Oldeman T-29*, leaves; and *Hoffman 2078*, wood and bark.

With the intent of searching for raphides in the various organs of this species, all the samples were rehydrated by boiling them in water. Subsequently, macerations were made by softening the tissues in equal volumes of acetic acid and 50% hydrogen peroxide. Wood and bark tissues were stained with Astra-blue, and flower and leaf tissues with Sudan IV. The prepared tissues were mounted on permanent slides, studied at the light microscope at regular light and with the aid of polarized lenses, and photographed using black and white film.

Taxonomic History

Aublet (1775: 196) characterized *Patima* by the hollow stems, axillary infructescences, and "4-, 5- or 6-locular" berries crowned by a persistent calyx. However, 4-locular berries have not been observed in the specimens examined, and it might be an erroneous report (Delprete, pers. obs.). Achille Richard (1830: 150) emended Aublet's description of *Patima*, and stated that (translated here from the French): "This genus [*Patima*] is very poorly known, since Aublet . . . observed only the fruit and not the flower; I have been very lucky to find a complete specimen of this plant in the rich herbarium of my friend M. Gay, collected in French Guiana by M. Poiteau, for the analysis of flower and fruit, which I have described above [in the generic description]. The genus *Patima* is not very distant from *Hamelia*, and it differs above all for the entire calyx, the shape of the corolla, and that of its stigma and anthers, and for the hairs that ornament the internal side of the corolla lobes." Richard included *Patima* in the Hamelieae [his "Hameliaceae"], among miscellaneous genera, a tribe he defined by (translated from the Latin) "fleshy fruits, often five-locular, locules many-seeded, and these [referring to the pyrenes of other groups of Rubiaceae] not bony nor dehiscent." The illustration drawn by A. Richard (Mém. Rubiacées, fig. 25, pl. 2) displays a bilobed style, while, according to our observations, the style of *Patima* is 5- or 6-lobed.

Candolle (1830) described *Patima forsythii* DC., which, in our opinion, does not belong to this genus but elsewhere in Rubiaceae; see Excluded Names.

Bentham (1841: 220) described *Patima laxiflora* Benth. based on depauperate material, and with the considerable mistakes of declaring that the flowers of this species are dioecious, and that the berries have (translated from Latin) "seeds very numerous, very minute, surrounded by a thin pulp." At the end of the description he added the note, "Of this I have seen two branches only, the one with a few male flowers half destroyed by worms, the other bearing two or three berries not yet ripe. On account of the remarkable structure of these fruits, I have placed the species under *Patima*; but perhaps the flowers when better known may show it to be a new allied genus."

Baillon (1880) began an unfortunate tradition by synonymizing *Patima guianensis* with *Sabicea* Aubl., and made the new combination *Sabicea guianensis* (Aubl.) Baill. In his narrative description of *Sabicea*, he stated, "The ovarian cells are often incomplete, and so also are those (five in number) of *Patima*, from Guyana, the calyx of which is truncate, and which, with us, forms a section of the genus *Sabicea*" (English edition; Baillon, 1881: 320).

Hooker (1873: 98), following Bentham's erroneous description of *Patima laxiflora*, synonymized this taxon with *Kutchubaea* Fisch., creating a mixed generic description, with the flower characters of *Kutchubaea* and the fruit characters of *Retiniphyllum* [referred herein to *Retiniphyllum laxiflorum* (Benth.) N. E. Br.]. In the description of *Kutchubaea* he correctly wrote that the flowers are dioecious and 8-merous, but he wrote that the fruit is a globose drupe, costate when dry, with 6 or 7, 3-angular, dorsally 3-costate pyrenes, which are characters of *Retiniphyllum* fruits (while in *Kutchubaea* the fruits are many-seeded, leathery berries; Delprete, pers. obs.).

Schumann (1889: 396–397), based on Bentham's (1841) and Hooker's (1873) incorrect generic descriptions, maintained *Patima* sensu Bentham synonymous with *Kutchubaea*, and *Patima laxiflora* with *Kutchubaea insignis* Fisch., the only species of this genus known to him. The erroneous synonymy of Hooker (1873) and Schumann (1889)

caused considerable confusion among the unrelated genera *Patima*, *Retiniphyllum*, and *Kutchubaea*, and this has unfortunately been repeated through the literature. In the same publication, Schumann (1889: 308–309) treated *Patima* sensu Aublet as a "poorly known" monospecific genus, and placed it next to *Sabicea*, citing Aublet's type of *P. guianensis*, acknowledging Baillon for sending two flowers of this specimen from the Paris Herbarium, but that unfortunately were insect-infested. In the same note, Schumann also stated that *Patima forsythii* would probably prove to be synonymous with *P. guianensis* (Schumann, 1889: 308): the taxon is excluded herein.

Although Schumann noted that Baillon treated *Patima* as synonymous with *Sabicea*, Schumann maintained *Patima* as a separate genus, although with some reservations, and indicated that future investigations were necessary in order to clarify the identity of these two genera. Additional collections that have been accumulated during the following century showed that *Patima* is easily distinguished from *Sabicea* by having flowers in fasciculate inflorescences, truncate calyx, very long-acuminate corolla lobes, and membranous-appendiculate anthers (vs. flowers in congested or cymose-corymbose inflorescences, lobed calyx, acute corolla lobes, and obtuse to shortly apiculate anthers in *Sabicea*; Delprete, pers. obs.).

Brown (1901: 36–37), with the help of additional, more complete collections [i.e., *im Thurm 6*, *McDowell & Quelch 18*, *Appun 1175*, *Rob. Schomburgk 724* (*Rich. Schomburgk 815*), *(?) Schomburgk 158*] elucidated the identity of *Patima laxiflora*, explained the mistakes of Bentham, Hooker, and Schumann, and clarified the distinction among *Patima*, *Retiniphyllum*, and *Kutchubaea* as follows: "This very distinct species of *Retiniphyllum* [i.e., *Patima laxiflora*] appears to have been misunderstood by all authors. Originally it was doubtfully referred by Bentham to the genus *Patima*, and erroneously described as having numerous seeds. Next, in Bentham and Hooker's *Genera Plantarum*, *ii* [Hooker, 1873: 98], it is confused with *Kutchubaea insignis* Fisch., and the part of the generic description in that work, relating to the fruit, is drawn up from the present plant and not from the true *Kutchubaea*, which indeed it greatly resembles in habit, but differs in having a 5-lobed corolla, 5 exserted, reflexed stamens, with long filaments, a long exserted style, and in the presence of a minute disk-like involucel at the apex of the pedicel, which is jointed to the calyx; while in *Kutchubaea* the corolla is 8-lobed, the stamens are 8, with the anthers almost sessile and included in the throat of the corolla tube, the style is included, and the pedicel is continuous with the calyx, without any trace of involucel" (Brown, 1901: 37).

Johnston (1924: 83) described *Patima formicaria* I. M. Johnst., stating that it is "evidently related to *P. guianensis* Aubl. . . . but having taller tetragonal stems, larger, long-acuminate leaves, larger flowers, and smaller apparently many-celled fruit." We concluded that the larger corollas of the type specimens are simply the fully expanded flowers in anthesis, and the other characters fit within the morphological range of *P. guianensis*.

Steyermark (1967: 314), clarifying the identity of *Sabicea guianensis* Wernham (nom. superfl.), wrote that this taxon is synonymous with *S. velutina* Benth., and should not be confused with *Sabicea guianensis* (Aubl.) Baill., which is in turn based on *Patima guianensis* Aubl. With this brief statement, it can be inferred that he recognized *Patima* as a distinct genus, not synonymous with *Sabicea*. However, in his Rubiaceae treatment for the *Flora of the Guayana Highlands* he did not provide any description or further explanation, although *Patima* occurs within the Guyana Shield.

Later, Robbrecht (1988, 1993[1994]) cited *Patima* as synonymous with *Sabicea*, but without presenting any rationale for it. Andersson (1992) also maintained *Patima* as synonymous with *Sabicea*, listing *P. formicaria* as synonymous with *S. formicaria* and *P. guianensis* as synonymous with *S. guianensis*, and suggested the intentionally invalid combination "*Sabicea formicaria* (I. M. Johnst.) comb. ined., cf. *Patima*" (1992: 150, 188). Four years later, Andersson included a handwritten note on the holotype specimen (at BM), of *Patima guianensis*, saying: "Calyx glabrous inside, without colleters; [. . .] ovary rotten and somewhat hard to interpret, obviously 2-locular with several ovules per locule, placenta probably subpeltate, no traces of sclerified endocarp; no traces of raphides, neither in the ovary, nor in leaf tissue, numerous large, tanniferous idioblasts in tissue, crystal sand idioblasts frequent in disk tissue. Conclusion: In spite of its odd appearance there is nothing to contradict that this is congeneric with *Sabicea*; Lennart Andersson, 20 December 1996."

The most curious synonym that we assign to *Patima guianensis* was described by Moldenke (1933) in the Verbenaceae. The holotype of *Aegiphila gleasonii* Moldenke has immature fruits with a persistent, truncate calyx, a trait common to both *Aegiphila* and *Patima*, and thus the collector and two other eminent botanists (i.e., N. E. Brown and Moldenke) mistook the specimen for an *Aegiphila*, as the holotype at NY bears (in sched.) a note by N.

E. Brown: "237, *Aegiphila*? Not matched at Kew nor the British Museum, Determinavit N. E. Brown, 1923." In a note glued on the type specimen, Moldenke reported: "Although only one leaf is present on the type specimen, the collector affirms that the leaves were opposite and that the fragment mounted alongside the larger specimen is a section of the same stem at the same node, showing the opposite glomerule and the petiole of the other member of the pair of leaves." He maintained *Aegiphila gleasonii* as a valid species endemic to Guyana through his last complete account of the accepted species of Verbenaceae (Moldenke, 1947, 1980), but soon afterward developed doubts. The holotype was originally labeled "TYPE: *Aegiphila gleasonii* Moldenke, Identified by H. N. Moldenke and cited by him in his monograph of the Genus, September 1929," as can be seen in the photo at NY taken of the holotype in 1929. Moldenke later removed his type annotation and pasted another in its place stating, "In spite of the opinion of Brown & Gleason, I do not now think this is an *Aegiphila* nor even anything verbenaceous. Still, nomenclaturally, it is the holotype of *Aegiphila gleasonii* Mold., Identified by H. N. Moldenke, April 1983." A search through over a hundred articles by Moldenke in his journal *Phytologia* after 1980 did not reveal any published account of his doubts, nor are there any further manuscript comments in the Moldenke herbarium now at TEX/LL (T. Wendt, pers. comm.). *Aegiphila gleasonii* was treated as an insufficiently known species by Jansen-Jacobs (1988) in the Verbenaceae treatment for the *Flora of the Guianas*. A close examination of the type specimen of this taxon reveals that between the opposite leaves there is a stipule scar (stipules absent in *Aegiphila*) and that the ovary is inferior (superior in *Aegiphila*), two important characters that immediately position this taxon in the Rubiaceae; in addition, the axillary, fasciculate infructescences, the 5-locular fruits, the bilamellate placenta, many-seeded placental extensions, the minute, globose seeds, and the truncate (minutely 5-denticulate) calyx indicate that this specimen is in fact a *Patima*.

Presence of Raphides and Systematic Placement of *Patima*, with Notes on the Circumscription and Position of the Tribe Hamelieae

The most recent list of the genera included in the tribe Hamelieae (Rubiaceae) was presented by Delprete (1998), as influenced by the phylogenetic study using morphological characters of Bremer (1987). According to recent phylogenies using *rbc*L (Bremer & Thulin, 1998) and *trn*L/*trn*L-F sequences (Rova et al., 2002), the tribe Hamelieae belongs to the subfamily Cinchonoideae, while *Sabicea* belongs to the tribe Sabiceeae of the subfamily Ixoroideae (Bremer & Thulin, 1998). The position of *Patima* using molecular phylogenies remains to be tested. Bremer (1987) excluded *Patima* (with many other genera) from the Hamelieae because of the absence of raphides. After a superficial search at the dissecting microscope, we tended to agree with Bremer's conclusion and Andersson's handwritten note about the absence of raphides in *Patima*, as they can normally be seen in thin tissues like leaf blades or corollas with the use of a regular hand lens; this was not the case with this taxon. Because of the proposed positioning of this genus in the Hamelieae, an exhaustive search for raphides was undertaken. After a careful study of the samples cited in Material and Methods, cells containing raphides in different amounts and sizes were found in several tissues. The length of the individual needles was 20–40 μm. Numerous raphides were found in the old calyx and developing fruit in *Henkel et al. 4941* (MO, U, US). They were also found arranged in long chains along the veins feeding the young fruit, and as single bundles in the old calyx lobes. However, they were not found in the corollas, neither in buds nor in anthesis, of *Granville & Crozier 13650* (CAY, MO[2], U). In the bark tissue of *Granville & Crozier 5829* (CAY, MO, NY, U, US[2]) and *Hoffman 2078* (U, US), raphides were in scanty, thick bundles of 20–40(–60) μm long needles in parenchyma cells (Fig. 1). In contrast, in the xylem cells they seemed to be absent. In the leaves of *Patima* the presence of raphides was observed to be sporadic: While in one leaf of *Oldeman T-29* a few raphides were seen in one of the secondary veins, in the leaf studied of *Granville & Crozier 13650* they were lacking. Therefore, in *Patima* raphides were found in the old calyx, developing fruit, and in the bark, while in other tissues they were observed to be extremely scanty or lacking. The finding of raphides in *Patima* should also be interpreted as an example for other Rubiaceae genera where the raphides have been declared absent; for these genera a detailed anatomical study of the various organs of the plant is recommended before the absence of raphides can be declared with sufficient confidence.

Summarizing, because of the overall morphological similarity with the members of the tribe, we position *Patima* in the Hamelieae, and we maintain this tribe in the subfamily Cinchonoideae, according to the molecular phylogenies cited above. Within the Hamelieae, *Patima* is most similar to *Hoffmannia* because of the commonly single-stemmed

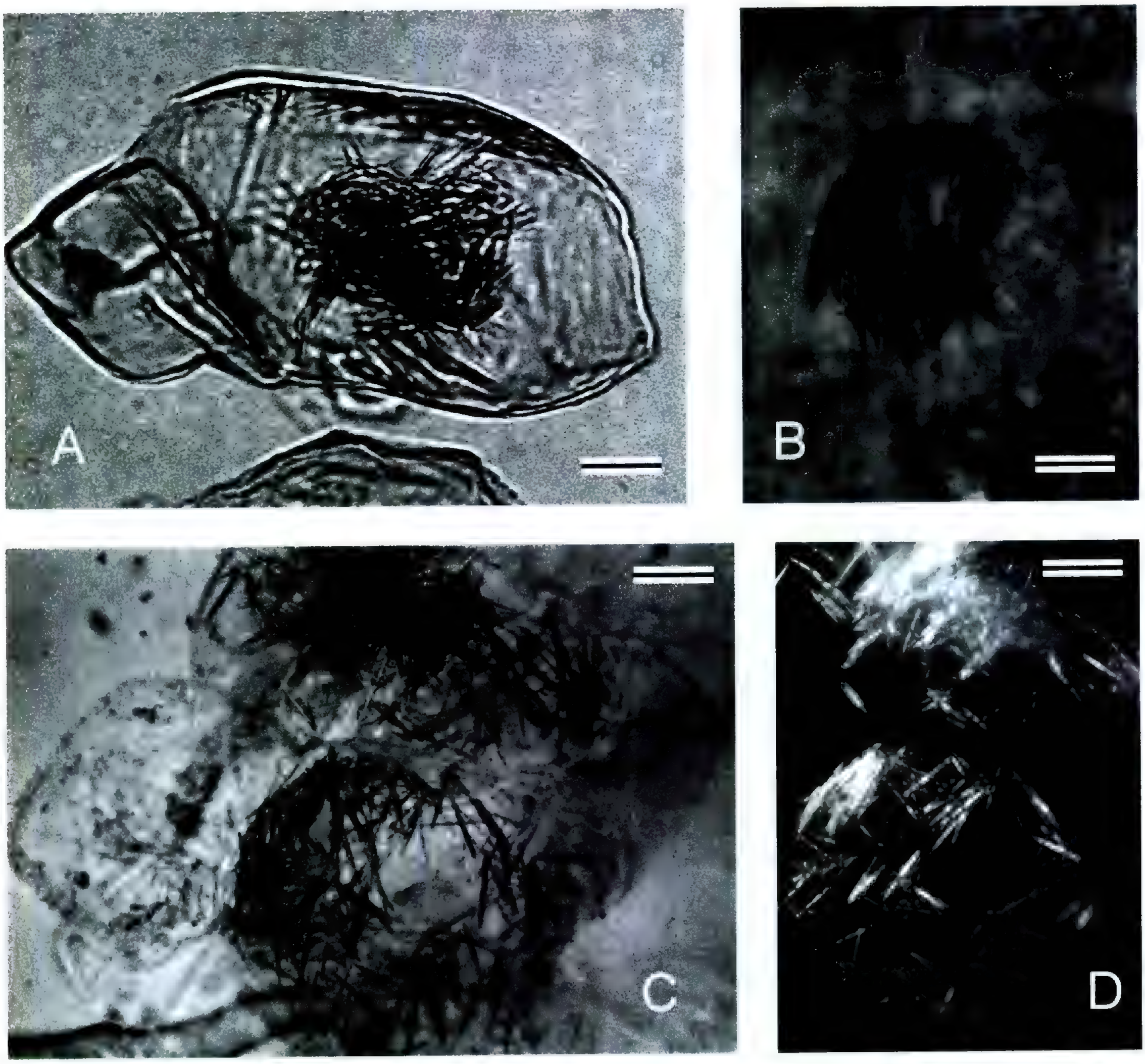
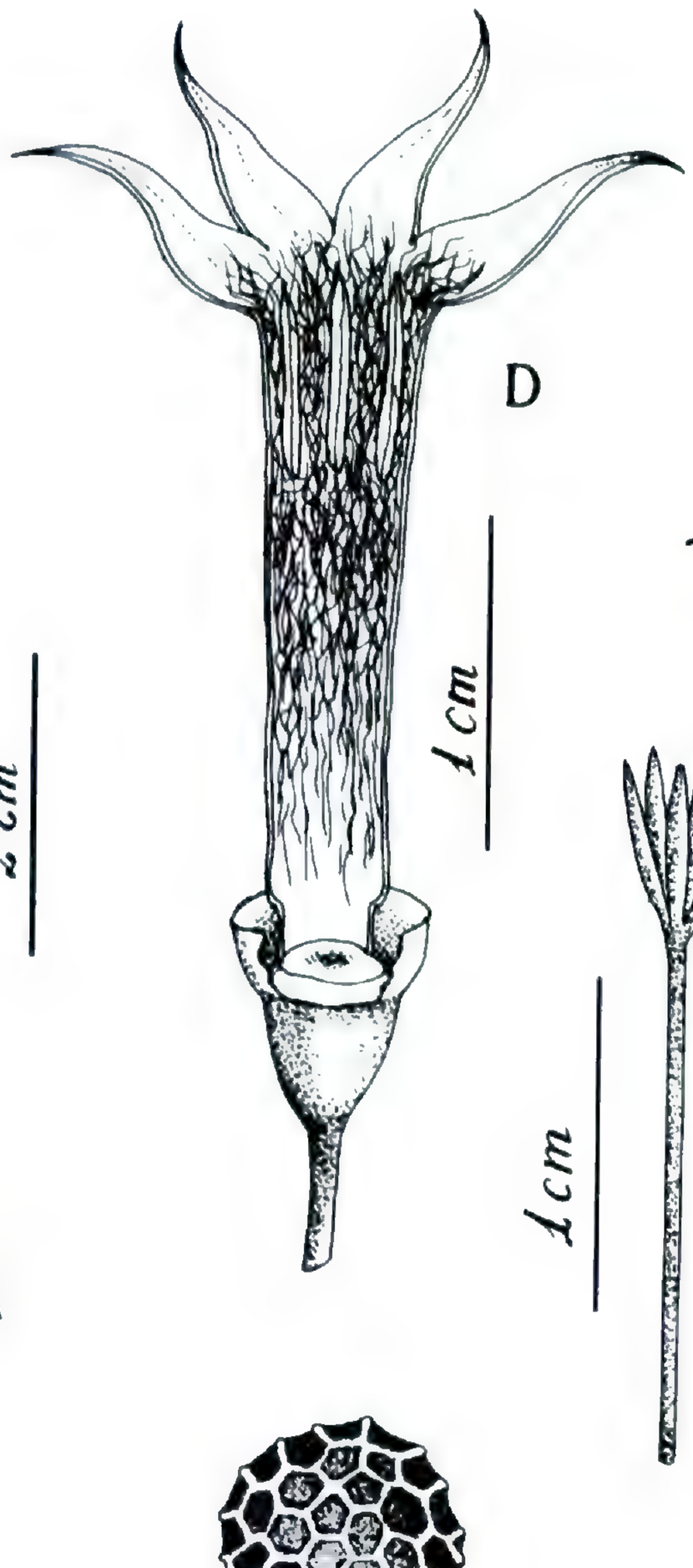
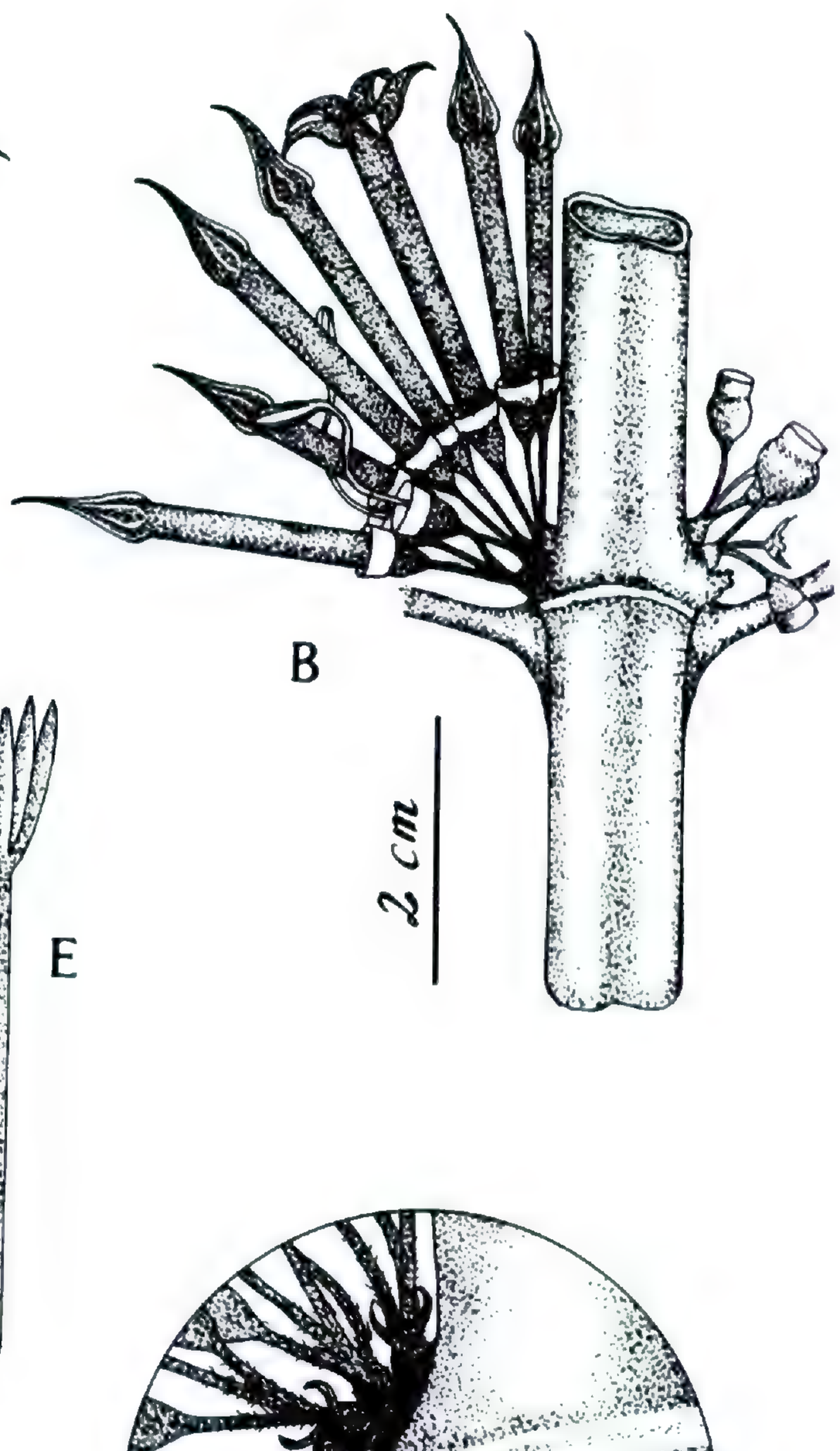


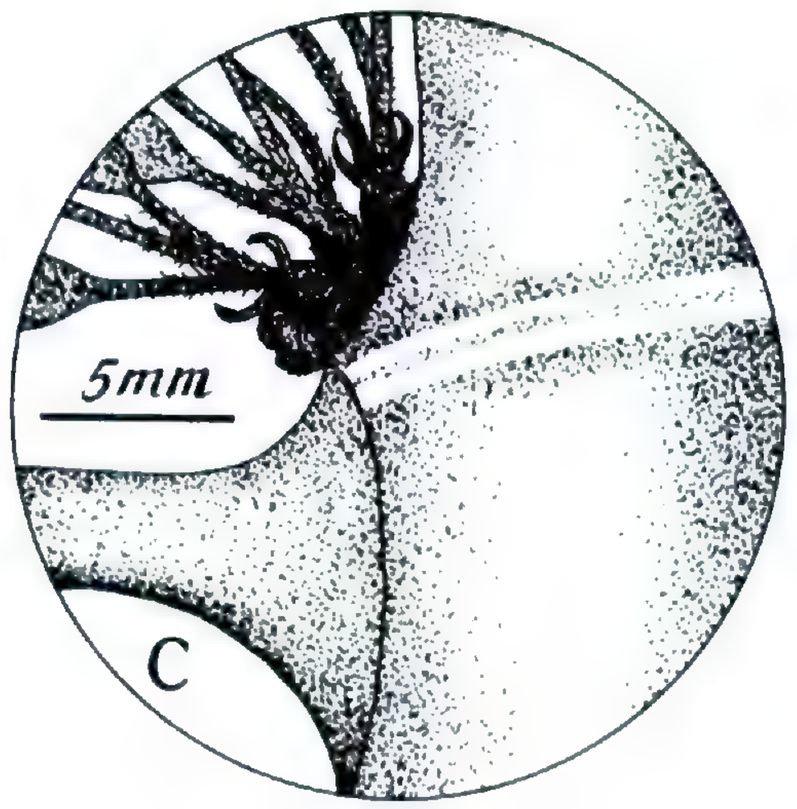
Figure 1. Raphides in bark cells of *Patima guianensis*.—A. Macerated parenchyma cell with raphides. —B. Unbleached tissue, showing nearly undamaged raphides. —C. Macerated parenchyma cells, showing squashed raphides. —D. Same as C, seen with polarized light. A photographed from *Granville & Crozier 5829* (U); B–D from *Hoffman 2078* (U). Scale bars: A = 25 μm, B–D = 13 μm.

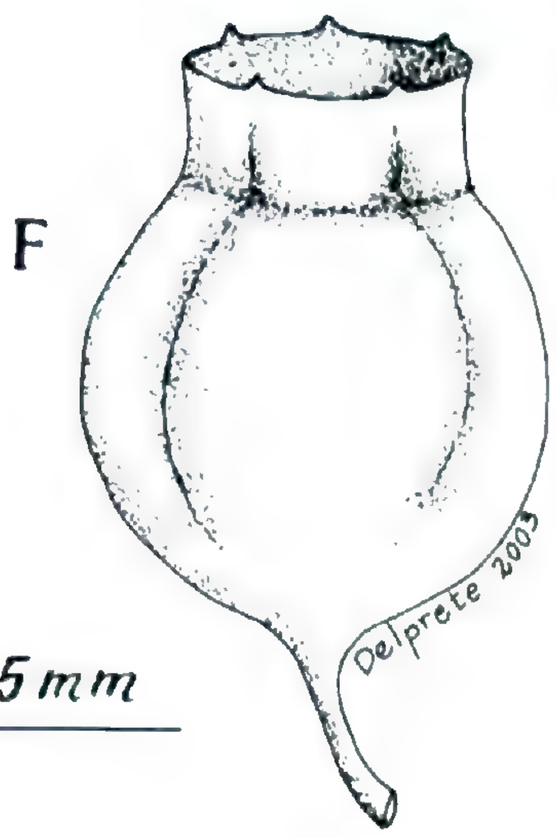
habit, hollow terminal internodes (in *Patima* and a few species of *Hoffmannia*, e.g., *H. vesciculifera* Standl.), axillary inflorescences, corolla with valvate aestivation, ovary locules with bilamellar placenta, and persistent calyx (see Fig. 2). The main morphological differences between *Patima* and *Hoffmannia* are summarized in Table 1.

In conclusion, herein according to Delprete (1998), the following genera are included in the Hamelieae: *Chione* DC. (1 sp., 4 var.; Taylor, 2003a), *Colleteria* D. W. Taylor (2 spp.; Taylor, 2003b), *Cosmocalyx* Standl. (1 sp.), *Deppea* Cham. & Schltdl. (24 spp., incl. *Schenkia* K. Schum.), *Eizia* Standl. (1 sp.), *Hamelia* Jacq. (17 spp.), *Hoffmannia* (ca. 100 spp.), *Omiltemia* Standl. (2 spp.), *Patima* (1 sp.), *Pinarophyllon* Brandegee (2 spp.), *Plocaniophyllon* Brandegee (1 sp.), and *Syringantha* Standl. (1 sp.). However, the generic delimitations and monophyly of this tribe remain to be tested with phylogenetic analyses. With this circumscription, the Hamelieae are a group mostly centered in Mexico and Central America, but with *Hamelia* and *Hoffmannia* extending to South America, *Deppea* with all the species in Mexico and Central America with the exception of *D. blumenaviensis* (K. Schum.) Lorence, endemic to southern Brazil (Santa Catarina and Rio Grande do Sul) and northern Argentina (Misiones), and with *Patima* being the only genus in the Hamelieae endemic to the Guayana Shield.









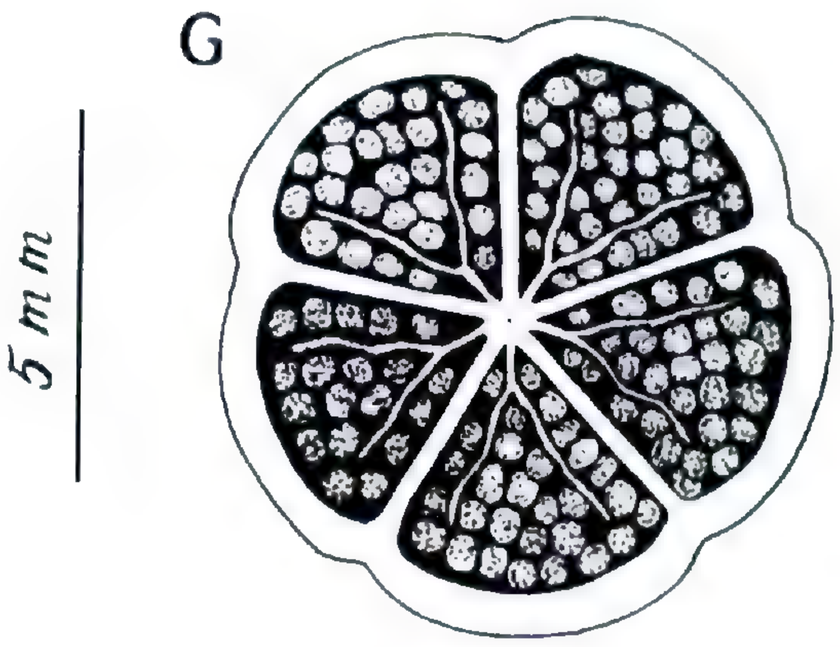


Figure 2. *Patima guianensis*.—A. Longitudinal section of the hollow stem; note the irregular entrance holes below the nodal septa. —B. Portion of stem with axillary inflorescence. —C. Detail of the inflorescence insertion. —D. Section of open flower, without style. —E. Style. —F. Fruit. —G. Cross section of a fruit; note stalked, bilamellar placentae. —H. Seed. A drawn from *Hoffman & Marco 2355* (NY); B–E from *Hoffman 2078* (US); F–H from *Maguire & Fanshawe 22968* (NY).

Table 1. Morphological differences between *Patima* and *Hoffmannia*.

	Patima	*Hoffmannia*
Calyx	truncate (lobes absent or minute teeth)	lobed (lobes narrowly triangular, acuminate)
Corolla merosity	5(6)-merous	(3)4(5)-merous
Ovary	5(6)-locular	2(3(4))-locular
Style	5(6)-lobed	2-lobed or clavate
Fruit shape	globose	oblong or ellipsoid (rarely subglobose)
Seed shape	globose	3- to 4-angular (rarely flattened)

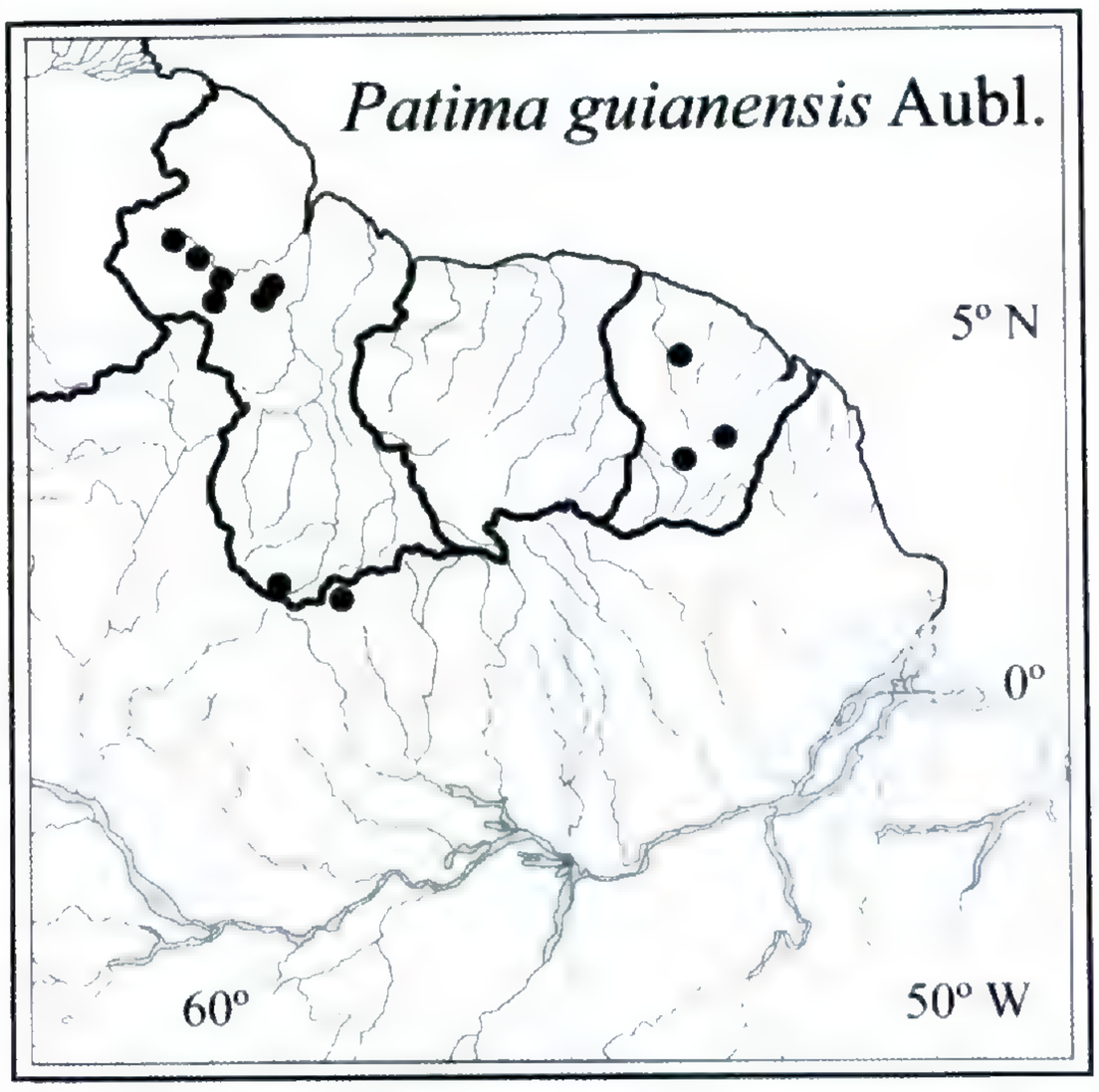


Figure 3. Distribution of *Patima guianensis* in the Guianas and northern Brazil.

Taxonomic Treatment

Patima Aubl., Hist. Pl. Guian. Franç. 1: 196. 1775. TYPE: *Patima guianensis* Aubl.

Single-stemmed plants, rarely with 1 or 2 branches; terminal internodes hollow; *raphides* present in the calyx, developing fruits, and bark, extremely rare or lacking in most other organs (e.g., leaf blades); *stipules* interpetiolar, free, basally deltoid and distally acuminate, persistent or subcaducous. *Leaves* opposite, long-petiolate; blades elliptic to oblong to oblanceolate, chartaceous or papyraceous; domatia of tufts of sparse hairs, or absent. *Inflorescences* axillary, supranodal, sessile, fasciculate, pauciflorous. *Flowers* bisexual, protandrous; *hypanthium* broadly obconical or globose; *calyx* cupular, truncate, persistent; *corolla* actinomorphic, salverform; tube externally glabrous, glabrous at base and sparsely pubescent at medio-distal portion inside; lobes 5 or 6(or 7), valvate, ovate at base, acuminate or caudate at apex; *stamens* alternate to the corolla lobes, included; filaments attached at the upper part of the corolla tube, free, complanate, shorter than the corolla tube, equal, glabrous; anthers narrowly oblong, rounded at base, acute at apex, dehiscing by longitudinal slits, dorsifixed near the base; *ovary* inferior, 5- or 6-locular; placenta with two lamellar extensions, with ovules attached throughout the entire length of the septum; ovules many per locule; *style* partially exserted (only tips of branches exserted), terete, glabrous; *style branches* 5 or 6, narrowly ovate. *Fruit* a globose berry, each locule with a bilamellar placenta, the mesocarp fleshy; *seeds* horizontal, minute, globose.

Patima guianensis Aubl., Hist. Pl. Guian. Franç. 1: 197, fig. 77 [as "*Patima guyannensis*"]. 1775. *Sabicea guianensis* (Aubl.) Baill., Hist. Pl. 7: 320. 1880. TYPE: French Guiana. Base of the mountain between the Galibis Creek and the Sinémari River, in swampy area, May [1762–1764] (fr), *J. B. C. F. Aublet s.n.* (holotype, BM!, photo at NY!). Figures 1, 2, 3.

Patima formicaria I. M. Johnst., Contr. Gray Herb., n. s. 70: 83. 1924. Syn. nov. TYPE: Guyana. Tumatumari, Potaro River, 5°20′N, June 1920 (fl), *A. S. Hitchcock 17348* (holotype, GH!; isotype, US!).

Aegiphila gleasonii Moldenke, Repert. Spec. Nov. Regni Veg. 33: 123. 1933. Syn nov. TYPE: Guyana. Upland bush of Potaro Landing [ca. 5°20′N, 59°13′W], Kangaruma, 25–27 June 1921 (fr), *H. A. Gleason 237* (holotype, NY!, photo at NY!; isotype, GH!).

Hoffmannia megistophylla Standl., in A. C. Smith, Lloydia 2: 214. 1939. Syn. nov. TYPE: Brazil. Pará: southern Akarai Mts., in drainage of Rio Mapuera (Rio Trombeta tributary), 500–700 m, 18–20 Jan. 1938 (fl), *A. C. Smith 2930* (holotype, F not seen; isotypes, MO 1163782!, NY!).

Plants to 2(–3(–4)) m tall; stems terete or faintly quadrangular, 0.7–2 cm diam., smooth, woody, glabrous throughout or puberulent at nodes; internodes hollow, frequently inhabited by ants, with minute, circular entrance holes just below the nodes; *stipules* 5–8 mm long, 5–9 mm wide at base, sparsely short-pubescent outside, densely pubescent and intermixed with colleters inside, subcaducous or short-persistent, leaving a scar encircling the stem just above petiole attachments. *Leaves* opposite (2 or 3 per node only *Tillet et al. 45018*), long-petiolate; petioles 5.5–13 cm long, canaliculate above,

± succulent when fresh, glabrous; blades elliptic, broadly elliptic, narrowly obovate, obovate, oblong, to oblanceolate, 18–53 × 7.5–22 cm, acute to decurrent at base, acute to obtuse at apex, chartaceous to papyraceous, dark green above, pale green below, drying pale brown, glabrous above, sparsely appressed-pubescent below; primary and secondary veins glabrous or sparsely pubescent above, sparsely appressed-pubescent and prominent below; secondary veins 16 to 26 on each side; tertiary veins subparallel-reticulate. *Inflorescences* (1)2- to 5-flowered, sometimes made of 2 or 3 units of (1)2 or 3(4) flowers, these subtended by 1 or 2 narrowly triangular bracts. *Flowers* long-pedicellate; pedicels thin and delicate, 5–8 mm long, glabrous or puberulent, slightly elongating to 8–14 mm at fruit maturity; *hypanthium* obovoid, ca. 2 mm long, minutely puberulent; *calyx* cupular, truncate, the margin sometimes slightly undulate, or rarely with minute teeth to 1.5 mm long, glabrous to very sparsely puberulent, without colleters inside; *flower buds* acute and caudate at apex, with valvate aestivation; *corolla* 2–3.1 cm long, pale yellow, yellow or pale greenish yellow; tube 1.7–2.3 cm long, 2.5–3.5 mm wide at base, 5–8 mm wide at mouth; corolla lobes 5 or 6(7), ovate at base and long-acuminate at apex, 5.5–6.5 mm long, glabrous throughout; *stamens* 5 or 6(to 7), included, of equal length; filaments attached 6–7 mm below the lobe sinuses; filaments 2.5–3.5 mm long, complanate, glabrous, anthers 3–3.5 × 0.3–0.4 mm; *style* with the lobes barely exserted just above lobe sinuses, terete, glabrous; lobes 5 or 6, narrowly ovate, stigmatic surface papillose. *Fruits* 5- or 6(7)-locular, globose, 6–9 × 5–9 mm when dry, crowned by the persistent calyx, yellow to orange at maturity, drying brown, smooth (not costate), glabrous; *seeds* ca. 0.3–0.5 mm diam.; exotesta deeply reticulate, the cells of regular shape, with (4)5 or 6 sides.

Distribution and habitat. Known from the eastern portion of the Guayana Shield, in Guyana, French Guiana, and northern Pará, Brazil, near the Guyana border (Fig. 3); on brown-sandy or lateritic soils, usually rich in organic material, or "scrub forest on white sand" (*Hoffman 2078*, U, US) of lowland rainforest, 80–760 m, in association with *Catostemma* Benth., *Oenocarpus* Mart., and *Bactris* Jacq. (*Clarke et al. 7297*, MO, NY, U, US). No collections are known from Surinam, but we anticipate that it also occurs there, at least in the southern portion of the country.

Phenology. Flowering specimens were collected in January, March, and June; fruiting specimens were collected in March and April and from June to December.

Additional specimens examined. FRENCH GUIANA. Ferme d'aquaculture sur La Comté, *Billiet & Jadin 4312* (BR, CAY, K, MO); route de Petit Saut, km 35, entrée vers Crique Plomb, *Billiet & Jadin 4806* (BR, CAY); Mont Chauve, *Cremers & Crozier 15024* (CAY, MO, U); Montagnes de la Trinité, N summit, creek margin, *Granville et al. 5829* (CAY, MO, NY, U, US[2]); Montagnes de la Trinité, zone sud, Bassin de la Mana, *Granville & Crozier 13650* (CAY, MO[2], U); D. Z. de Saut Aïmara, Bassin du Sinnamary, *Hoff 6945* (MO); Approuague River, trail to Saut Grand Canori, *Oldeman T-5* (NY); Approuague River, R margin of the Saut Grand Canori, *Oldeman T-29* (NY, U, US); Saül Region, Saut Mais, 17 km E of Saül, on islands and banks of river, *Skog et al. 7237* (NY, US). GUYANA. Region Upper Takutu-Upper Essequibo River, Acarai Mts., 8 km S of Sipu River, camp at base of highest peak in central Acarai Mts., *Clarke et al. 7297* (MO, NY, U, US); Region Takutu River-Essequibo River, Acarai Mts., Tinarnau Creek at NW base of Tinarnau Peak, *Henkel et al. 4941* (MO, U, US); Upper Takutu-Upper Esequibo Region, S Pakaraima Mts., 5 km E of Tipuru Village, lower ridge of Mt. Ureisha, *Hoffman & Jacobs 1163* (MO); Cuyuni-Mazaruni Region, Pakaraima Mts., Kurupung River, landing at base of Makreba Falls, *Hoffman 2078* (U, US); Cuyuni-Mazaruni Region, Pakaraima Mts., Upper Meamu River, *Hoffman & Marco 2355* (NY, US); Rupununi District, S edge of Pakaraima Mts., Ureisha Mt., summit ca. 5 hr. walk above Tipuru Village, *Knapp & Mallet 2860* (MO); Upper Mazaruni River, Kamakusa, *Lang 78* (NY); clayey hills at mouth of Merumé Creek, near Kamakusa, *Lang 330* (GH), 8 Dec. 1922 (fr), *Lang 339* (GH, US); Potaro River, Garraway Stream, *Maguire & Fanshawe 22968* (NY); Potaro-Siparuni Region, along trail up Eagle Mt., 2–3 km above junction with Potaro–Konowaruk Rd., *McDowell & Gopaul 3439* (NY, U, US); Cuyuni-Mazaruni Region, E side, confluence of Eping and NW branch Eping River, *McDowell & Stobey 3826* (US); Upper Mazaruni River Basin, below talus of cliffs along NE side, *Tillett et al. 45018* (NY).

Common names. Patima-rana (Carib; Aublet, 1775: 197), Patime de la Guiane (French; Aublet, 1775: 197).

Ant/Plant interaction

In describing *Patima formicaria*, Johnston (1924: 83) stated, "According to Dr. W. M. Wheeler, to whom the Gray Herbarium is in debt for excellent material of the species, the plant is myrmecophilous, its fistulous stems being the habitation of at least five species of ants." The name *Patima formicaria* was used also by Jolivet (1996), who reported that the hollow internodes are inhabited by ants and that the entrance hole is located just below the nodes (Delprete & Crozier, pers. obs. in French Guiana). The specimen label of *McDowell & Stobey 3826* (US) reports that this species has "stem hollow with ants and eggs within (ants ± 2 mm long)." In addition, Jolivet (1996)

reported that six species of ants were found living in the internodes of *P. guianensis*, among them *Azteca traili* and two species of *Camponotus*, and suggested that the ants "are responsible for opening the entrance pores and for the destruction of the nodal septa." In addition, Ward (1991: 341) reported that the hollow stems of *Patima* are inhabited by ants of the species *Pseudomyrmex tenuis*. At least one species of *Hoffmannia*, *H. vesciculifera* Standl., from Central America, has hollow terminal internodes that Jolivet (1996) reported to be inhabited by ants of the genus *Solenopsis*.

Excluded Species

Patima forsythii DC., Prodr. 4: 444. 1830. TYPE: Locality and collection date unknown, (fr), [?] *Forsyth 189* (holotype, G-DC!; photos at NY!).

Candolle (1830: 444) published *Patima forsythii* with the short and vague description (liberal translation from Latin): "Leaves petiolate, raceme pauciflorous and longer than petiole, locality and flowers unknown, communicated by Forsyth with the name *P. guianensis*, but according to my observation different from Aublet's illustration (if correctly drawn), although without flowers or fruits." The identity of the collector and the collection locality of the type are dubious, and an assessment of the taxonomic position of the depauperate type is difficult. The specimen has two opposite leaves, a short inflorescence, three enlarged ovaries crowned by a truncate calyx with five minute teeth, and no corollas. Because of the opposite leaves and the deltoid stipule, the specimen evidently belongs to the Rubiaceae, but other characters indicate that it is not a *Patima*: The petioles are ca. 5–7 mm long (vs. 5.5–7.5 cm long in *Patima*), the inflorescence is racemose, with a few-branched rachis (vs. rachis absent), and one of the pedicels has two sub-alternate bracteoles at the medial portion (vs. bracteoles lacking). Because of the absence of flowers, it is impossible to assign this taxon to any other rubiaceous genus with certainty.

Patima laxiflora Benth., J. Bot. (Hooker) 3: 220. 1841. TYPE: Guyana. [Roraima, 1838], *Rob. Schomburgk 158.S* (lectotype, designated here, K 2139!; isotype, K 2138!) [= *Retiniphyllum laxiflorum* (Benth.) N. E. Br.].

Of the two type specimens preserved at K, the one with n. 2139 is a more complete specimen and bears Bentham's handwriting.

Bentham (1841: 220) described *Patima laxiflora* because of the 5-locular immature fruits of the type specimens, and added the note "I have placed the species under *Patima*; but perhaps the flowers when better known, may show it to be a new allied genus." As explained above, Bentham was dealing with insect-infested fruits, which caused him to believe that they had many-seeded locules. However, Bentham should at least have noticed that this species has terminal inflorescences and flowers subtended by involucels, which are two generic characters peculiar to *Retiniphyllum* Humb. & Bonpl. (vs. inflorescence terminal and flowers without involucels in *Patima*). Six decades later, Brown (1901), helped by more complete collections, corrected Bentham's mistakes and transferred *Patima laxiflora* to *Retiniphyllum*, a decision with which we and R. Cortés-B. (2003) agree.

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A REVIEW OF HYBRIDIZATION IN NORTH AMERICAN HAWTHORNS—ANOTHER LOOK AT "THE *CRATAEGUS* PROBLEM"[1]

J. B. Phipps[2]

ABSTRACT

The study of nearly 400 syntype, other type, and probable type elements of *Crataegus*, in the context of over 4000 other Missouri specimens examined for the Flora of Missouri Project, provided a unique opportunity to look at putative hybridization in the Missouri *Crataegus* flora. These specimens collectively represent essentially all the taxonomic variation observed to date for the state. Each type specimen was studied and then categorized as being either: (a) a primary species (orthospecies); (b) a synonym of an orthospecies; or (c) representing a wide hybrid (nothospecies). These nothospecies, all putative, constitute the totality of alleged hybrids for Missouri. Computation of hybrid frequency yielded the conclusion that wide hybrids occur between about 15% of the possible interserial combinations, and field and herbarium studies show that populations of these hybrids are usually small and non-persistent. Working with weaker data, roughly similar results were generated for the whole of the *Crataegus*-rich northeastern quadrant of the United States (and adjacent Canada). Interestingly, the very small surviving, or even extinct, nature of the populations of these hybrids, together with their high reliability of correct identification, indicate that known hybrids do not contribute significantly to "The *Crataegus* Problem" routinely touted by North American authors.

Key words: *Crataegus*, frequency, hybridization, Missouri, North America, Rosaceae.

Every so often a paradigm requires review and such does the issue of hybridization in *Crataegus* L. Hybridization (as well as apomixis and polyploidy) has been repeatedly suggested by floristicians (e.g., Elias, 1989; Gleason & Cronquist, 1963, 1991; Little, 1979; Voss, 1985) as a root cause of the taxonomic complexity in *Crataegus* of North America. This is, in part, strange because absolute proof of hybridization on this continent is arguably non-existent and detailed investigations of putative hybrid situations extremely few. Indeed, where adequate documentation exists, two of the only three such situations actually involve the introduced species *C. monogyna* Jacq., firstly, with *C. suksdorfii* (Sarg.) Kruschke, as *C. douglasii* Lindl. var. *suksdorfii* Sarg. (Love & Feigen, 1979), and secondly, with *C. punctata* Jacq. (Wells & Phipps, 1989), while only one case, *C. rufula* Sarg. (Phipps, 1988), involves two native parents.

The Love and Feigen (1979) paper reports a careful morphometric study of hybrid populations of *C. douglasii* var. *suksdorfii* × *C. monogyna* in the Willamette valley, Oregon. This was supplemented by fruit set studies following artificial crosses and pollen viability observations. The authors correctly claimed this as the first documented case of hybridization in *Crataegus* in North America, though they noted that they knew about my suspicion of *C. monogyna* × *C. punctata* crosses in Ontario. Interestingly, *C. monogyna*, which has become locally common in the Pacific Northwest, is now known to have given rise to other hybrid populations of the same parentage. The Wells and Phipps (1989) case represents a similar but more detailed study, in this case of *C. monogyna* × *C. punctata*, at the six then-known sites in southern Ontario, a region where both parents are common. In this study chromatographic profiles of leaf phenolic compounds and multivariate analysis of morphological features were incorporated. In all cases

[1] I thank George Yatskievych, Missouri Botanical Garden and Missouri Department of Conservation, for arranging to make available to me nearly 400 type sheets of species directly relevant to the systematics of Missouri *Crataegus*. It was this opportunity that first really focused my mind on the significance of interserial hybridization in North American hawthorns. George Yatskievych was particularly helpful in making available *Crataegus* database information and for providing useful comments on early drafts of this manuscript. I also thank my colleagues Paul Cavers and Dianne Fahselt for commenting on later manuscript drafts. This work was funded through the Natural Sciences and Engineering Research Council of Canada Discovery Grant A-1726 to the author and by the Missouri Department of Conservation, which supported several visits to St. Louis for the study of Missouri *Crataegus*.

[2] The University of Western Ontario, Department of Biology, 1151 Richmond Street, London, Ontario, Canada, N6A 5B7. jphipps@uwo.ca.

experimental crosses yielded fewer seeds than open pollination. Both of these cases represent extremely wide hybrids according to current notions of *Crataegus* taxonomy, and all three parental species are sexual diploids.

The *Crataegus rufula* case (Phipps, 1988) is somewhat different. It is based on a battery of morphometric analyses, all supporting the same result, on herbarium specimens of the putative parents and hybrid. The two parental species are almost perfectly allopatric. One, *Crataegus aestivalis* (Walter) Torr. & A. Gray (eastern mayhaw), extends through the coastal plain from southeastern Alabama and the Florida panhandle to coastal North Carolina, while the other, *C. opaca* Hook. & Arn. (western mayhaw), occurs from eastern Texas to the Florida panhandle in which latter area, together with extreme southwestern Georgia, *C. rufula* occurs. *Crataegus opaca* and *C. aestivalis* are very different from one another and most putative hybrid individuals are unequivocally identifiable as such. This case perhaps suggests old but persisting hybrid populations, or else repeated regeneration of the hybrid, because *C. rufula* has been known continuously from the time of its description by Sargent up to the present. The chromosome number of mayhaw is not reported, but the ease with which breeders can cross them suggests sexuality. The *Crataegus rufula* case is different from the two involving *C. monogyna* in that the hybrid is less wide, being intraserial, even though the parental species are quite distinct.

Support for the hybridization hypothesis historically derived from the understanding that the genus is taxonomically complex, that apomixis and hybridization are often intertwined, as well as from specific suggestions as to what taxa might be hybrid, these deriving mainly from Palmer (1952), Gleason and Cronquist (1963, 1991), and myself, as presented in this paper. The putative hybrids concerned are, however, quite numerous and the entities involved were originally noted during the heyday (about 1890–1930) of North American hawthorn discovery. Study of them reveals the following facts. All are hybrids between species belonging to different series (Tables 1, 2, and 3), as is discussed in the next paragraph. None of them are common, indeed, few are known today. Most, in fact, appear to be transient. My main examples come from Missouri.

The thinking behind this paper was catalyzed by a detailed study of *Crataegus* (unpublished) for George Yatskievych's new *Steyermark's Flora of Missouri* (vol. 2 in prep.). Being well aware of the taxonomic difficulties in *Crataegus*, I was pleased to have the opportunity to undertake so thorough a study. The huge MO collections (over 4000 sheets) were placed at my disposal and 384 type, isotype, syntype, and putative types were made available so that every taxon named from the state could be studied in detail. The resulting taxonomic revision will appear in a later volume of the flora, and all species names with types described from the state will be lectotypified or neotypified as appropriate (Phipps et al., in prep.). This revisionary activity has enabled me to see all of the Missouri material on which hybrid claims have been based and to evaluate collection frequency. In addition, my extensive studies and fieldwork in North American *Crataegus*, summarized provisionally in *Hawthorns and Medlars* (Phipps et al., 2003), also oblige me to the view, shared as well by Palmer (1943), that recognized putative hybrids are rarely encountered in the field.

The value of the Missouri data lies in that state's rich association with *Crataegus* taxonomy, the collectors Bush, Davis, Eggert, Kellogg, Letterman, and the systematist Engelmann all being active in the latter part of the 19th and the early part of the 20th centuries and collectively furnishing Charles Sargent at the Arnold Arboretum with thousands of specimens that were the source material for his (Sargent, 1908a) monumental "*Crataegus* in Missouri" with its later supplement (Sargent, 1912). Following the aforementioned group of hawthorn collectors in Missouri was the *Crataegus* expert E. J. Palmer. His early relationship with *Crataegus* also began as a collector in that state, which later translated to his own taxonomic studies of the genus across approximately the second quarter of the 20th century (e.g., Palmer, 1925, 1932, 1943, 1946, 1952, 1963). Only a few parts of North America can boast quite the degree of attention received by Missouri from Crataegophiles, although New York, Pennsylvania, Michigan, and Ontario also have a rich association with *Crataegus* (e.g., Sargent, 1903, 1905b, 1907, 1908b, c, d, 1913), as does Wisconsin with Kruschke (1965).

It has been customary in North American *Crataegus* taxonomy to generate stratification by placing small sets of similar species in the finest available division of the generic rank rather than by using bigger, more broadly defined groups. About a hundred years ago these small sets were called "natural groups" (e.g., Beadle, 1903; Rehder, 1904; Sargent, 1905a, and many other examples) or even left unnamed. Since Rehder (1940), however, these sets of related species have been usually assigned the formal taxonomic rank "series," although a few authors (e.g., Dickinson, 1985) preferred the next

higher rank "section." My preference is to use series for this lowest rank, because this permits further stratification by grouping series into sections. As a result, and for the purposes of this paper, wide crosses within *Crataegus* are deemed to be those between members of different series, i.e., interserial hybrids. The restriction of hybrids in this paper to wide or interserial hybrids is not, however, a convenient artifice, but a direct recognition that no others are specifically suspected among the instances discussed. Nevertheless, I must make it quite clear that I consider the investigation of the possibility of hybridization within species-complexes and between closely related species a particularly important avenue of future investigation in *Crataegus* as is also the possibility that some whole series may perhaps be hybrids. Examples of this are series *Silvicolae* (Beadle ex Sarg.) E. J. Palmer (possibly ser. *Pruinosae* Sarg. ex Rehder × ser. *Tenuifoliae* (Sarg. ex Eggl.) Rehder) and series *Brainerdianae* Eggl. ex E. J. Palmer (if hybrid, likely at least in part ser. *Macracanthae* (Loudon) Rehder × ser. *Tenuifoliae*, or ser. *Macracanthae* × ser. *Pruinosae*), and perhaps series *Dilatatae* Sarg. ex Rehder (possibly ser. *Pruinosae* × ser. *Molles* (Sarg. ex C. K. Schneid.) Rehder or series *Pruinosae* × ser. *Coccineae* (Loudon) Rehder, which, if demonstrated, would require recalculation of the frequency value. Series *Dilatatae* was investigated for hybridity by T. C. Wells (1985), but no firm conclusion could be drawn.

One must also bear in mind the somewhat unlikely caveats that some of the putative interserial hybrids might eventually not pan out as hybrid when tested rigorously and also that other possible wide hybrid cases are necessarily so far only suspected. On the other hand, it is almost inconceivable that a wide hybrid might be overlooked on the grounds of dominance-recessive relationships being systematically skewed toward one parent, because experience shows that hybrid indices developed from sufficiently numerous characters are robust. Therefore, bearing in mind these minor caveats, I feel confident that the degree of scrutiny to which the Missouri *Crataegus* flora has been subjected by specialists open to the hypothesis of hybridity makes it probable that the count of interserial hybrids, the only ones suspected for the state, is reasonably robust.

In this review, I start by discussing the problem of the detection of hybrid situations and the distinction between putative and proven cases. I will then consider the frequency of putative hybridization in Missouri, a state where the *Crataegus* population and *Crataegus* taxonomy has been studied in particular depth but from which, nevertheless, there are no proven examples. These findings are then extended to the whole of northeastern North America where, however, the supporting evidence is less detailed. Next, I present an overview of the development of views on hybridization in North American *Crataegus*, followed by a short account of barriers to hybridization (isolating mechanisms) that might be germane. I will finish with a discussion of the relevance of these new insights to the writing of floras.

Detection and Proof of Hybridity

Hybrids between species of flowering plants are generally suspected in the first place because of morphological intermediacy between the putative parents. Support for the hybrid hypothesis is strengthened when there is sympatry and similar floral phenology, without which natural hybrids cannot be created. Obviously, hybrids between morphologically very similar species are far less likely to be suspected than hybrids between more different species because in the former case the new variation created by the existence of the hybrid would be more nearly continuous with the parents. Also one is, of course, more readily led to a conjecture of hybridity in the case of relatively rare populations apparently intermediate between two sympatric species than one is with much more abundant intermediate populations with good fitness that might masquerade as orthospecies, and could, therefore, be overlooked as hybrid. This is perhaps the case for taxa in series *Brainerdianae* and series *Silvicolae*. In line with this thinking, it turns out that all putative hybrids in Missouri are derived from interserial crosses, and narrower, intraserial hybrids, if they exist, are not to date specifically suspected. For these reasons, therefore, this restriction is tantamount to limiting hybrid cases to interserial hybridization. And, as I have noted earlier, I use the term "interserial hybrids" in this paper not because no others might exist, but because no others have so far been predicated for the study region. Thus, reasonably wide hybrids are likely to be detected by a gestalt approach, the only level of inference so far employed for Missouri hawthorns. Although occasional intraserial hybrids in series of unusually wide amplitude (e.g., Phipps, 1988) might also occur and be recognized in Missouri, there are no such instances suggested here.

The ability to perceive a hybrid gestalt at all accurately is, of course, dependent on that individual's general taxonomic skills as well as his or her familiarity not only with the putative parents but

his or her awareness of other possible hybrid combinations in the taxon involved, in this case, *Crataegus*. It obviously also involves an openness to the possibility of hybridization, which explains why with Sargent only two "intermediate" situations were touted among the 732 (Macklin et al., 2002) species of *Crataegus* he described and, with Kruschke, none. But see more on Sargent's views later in this paper. The step from "putative" to "proven" hybrid is only rarely made, as it is relatively cost- and labor-intensive and most workers are willing to accept as likely the putative hybrid of experts.

A more convincing level of persuasion than the gestalt intermediacy of *Crataegus* experts arises if numerous characteristics (e.g., morphological, phytochemical, etc.) are investigated and intermediacy is unequivocally demonstrated by hybrid indices, or chromatographic patterns, etc. (e.g., Love & Feigen, 1979; Phipps, 1988; Wells & Phipps, 1989), but, as pointed out earlier, these cases are few in number in North America and two of these three cases involve *C. monogyna*, a European introduction already notorious in Europe for its freely hybridizing nature and dubbed a "compilospecies" by Christensen (1992).

One may eventually need to seek absolute proof of hybridity, which can only be generated experimentally by recreating the putative hybrid and proving conspecificity with the putative nothospecies or by genomic analysis identifying parental genomes in the hybrid. I do not know of any case of such stringent proof in North American *Crataegus*, although with horticulturally generated hybrids, for instance, *C.* ×*lavallei* Hér. and *C.* ×*grignonensis* Mouillef. ex anon. (see Phipps et al., 2003), which do not, in any case, contribute to the Missouri picture, there sometimes exists documentary evidence of origin, at least as to the female parent.

Numbers of Putative Interserial Hybrid Taxa of *Crataegus* in Missouri and North America

In this paper I utilize the list of putative hybrids for Missouri proposed by E. J. Palmer (1952), as amended by myself in this paper, and that by Cronquist (in Gleason & Cronquist, 1991) for northeastern North America (Tables 1–3). I have studied material of all of Palmer's putative hybrids that occur in Missouri. However, the putative hybrids proposed by Cronquist perhaps have more ambiguity, as he left no recorded research papers on *Crataegus* and his taxonomy broadly accepts as species the series of other workers, therefore bespeaking a certain procrustean, but convenient simplicity.

Study of over 384 syntype and other type specimens revealed that there were 120 *Crataegus* names described from Missouri and that about 104 of these names could easily be accommodated within standard views of about 26 orthospecies (Table 4) of Missourian *Crataegus*, while 22 names (Tables 1, 3) represented putative hybrids. There are a further 19 orthospecies of *Crataegus* found in Missouri but whose type occurs outside Missouri, indicating a total of 120 + 19 = 139 relevant *Crataegus* binomials for the state flora.

There are various ways in which hybrid frequency might be assessed. First, one might count all hybrid names and divide by the total of relevant binomials. The Missouri data would then show that 22/139 = 15% of the species names with types from the state are interserial hybrids or synonyms of them and the other 85% are orthospecies, synonyms of them, or lower taxonomic ranks within orthospecies. Second, one might take the approach whereby the number of accepted hybrid species is divided by that of all accepted orthospecies and nothospecies. Then, if the 22 taxa that are putative interserial hybrids are each treated as distinct species, the fraction of Missouri taxa of *Crataegus* that are interserial hybrids may be suggested to be 22/(22 + 26), i.e., approximately 48%. This is a huge but perhaps misleading value due to the somewhat different criteria used for numerator and denominator and exaggerates, I would argue, the importance of hybridization.

I therefore suggest that the most relevant statistic for estimating the frequency of interserial hybrids is a third approach whereby the number of different putative interserial combinations is expressed as a fraction of all possible interserial combinations. We may call this hybrid fraction "F," such that $F = x/[(n^2 - n)/2]$ where x = the number of putative hybrid cases suspected derived from different interserial combinations and n = the number of series. For Missouri, $x = 13$ by inspection of Table 5 while n (Table 4) is 14 (Palmer, 1963). Therefore, $x/[(n^2 - n)/2] = 14\%$. The hybrid combinations are summarized in Figure 1. It is interesting that essentially the same hybrid frequency is adduced using a splitting (15%) or a lumping (14%) taxonomy. A potential upper limit to F could be obtained by adding putative hybrids with only one parental series indicated such that $x > 15$ for Missouri when F = 16.5%, a slightly different value.

It should be pointed out that the value F obtained in the formula would obviously increase if the study added further constraints, e.g., local, rather than statewide sympatry or restriction to cases of overlapping anthesis phenology. With a flowering

Table 1. Putative interserial hybrids of *Crataegus* for northeastern United States and adjacent Canada in Palmer (1952). Asterisk = found in Missouri.

Name of taxon	Presumed parental species acc. to E.J.P.	Parental series
**C. danielsii* E. J. Palmer	(*crus-galli* × *collina*)	(*Crus-galli* × *Punctatae*)
C. persimilis Sarg.	(*succulenta* × unspecified)	(*Macracanthae* × *Crus-galli*)
**C. collicola* Ashe	(*collina* × *crus-galli*)	(*Crus-galli* × *Punctatae*)
C. disperma Ashe	(*crus-galli* × *punctata*)	(*Crus-galli* × *Punctatae*)
**C. incaedua* Sarg.	(*calpodendron* × *collina*)	(*Macracanthae* × *Punctatae*)
C. puberis Sarg.	(*punctata* × *macrosperma*)	(*Punctatae* × *Tenuifoliae*)
C. nitidula Sarg.	(unspecified × unspecified)	(*Punctatae* × *Rotundifoliae*)
C. kellermanii Sarg.	(*punctata* × unspecified)	(*Punctatae* × *Pruinosae*)
C. sylvestris Sarg.	(*punctata* × unspecified)	(*Punctatae* × *Pruinosae*)
C. desueta Sarg.	(*punctata* × ?)	(*Punctatae* × ?)
C. celsa Sarg.	(*punctata* × *succulenta*)	(*Punctatae* × *Macracanthae*)
C. pilosa Sarg.	(unspecified × unspecified)	(*Intricatae* × *Pruinosae*)
C. immanis Sarg.	(*dodgei* × *pruinosa*)	(*Rotundifoliae* × *Pruinosae*)
C. kingstonensis Sarg.	(*brainerdii* × *dilatata*)	(*Brainerdianae* × *Dilatatae*)
C. kennedyi Sarg.	(*brainerdii* × *jesupii*)	(*Brainerdianae* × *Silvicolae*)
C. vittata Ashe	(*macrosperma* × *pedicellata*)	(*Tenuifolia* × *Coccineae*)
C. merita Sarg.	(*macrosperma* × *pedicellata*)	(*Tenuifoliae* × *Coccineae*)
C. haemocarpa Ashe	(unspecified × unspecified)	(*Tenuifolia* × *Pruinosae*)
C. fretalis Sarg.	(*macrosperma* × unspecified)	(*Tenuifoliae* × *Coccineae*)
C. lucorum Sarg.	(*macrosperma* × unspecified)	(*Tenuifoliae* × *Coccineae*)
C. densiflora Sarg.	(*macrosperma* × *brunetiana*)	(*Tenuifoliae* × *Coccineae*)
C. media Sarg.	(unspecified × unspecified)	(*Silvicolae* × *Pruinosae*)
C. xanthophylla Sarg.	(unspecified × unspecified)	(*Silvicolae* × *Coccineae*)
C. formosa Sarg.	(unspecified × unspecified)	(*Pruinosae* × *Silvicolae*)
C. glareosa Ashe	(*pruinosa* × *succulenta* v. *michiganensis*)	(*Pruinosae* × *Macracanthae*)
C. durobrivensis Sarg.	(unspecified × *suborbiculata*)	(? × *Pruinosae*)
C. littoralis Sarg.	(*pruinosa* × *intricata*)	(*Pruinosae* × *Intricatae*)
**C. locuples* Sarg.	(unspecified × *mollis*)	(*Pruinosae* × *Molles*)
C. corusca	(unspecified × *mollis*)	(*Coccineae* × *Molles*)
C. illecebrosa Sarg.	(*pedicellata* × *dilatata*)	(*Coccineae* × *Dilatatae*)
**C. kelloggii* Sarg.	(*margaretta* × *mollis*)	(*Rotundifoliae* × *Molles*)
**C. latebrosa* Sarg.	(*noelensis* × *collina*)	(*Molles* × *Punctatae*)
C. aulica Sarg.	(*dilatata* × unspecified)	(*Dilatatae* × *Coccineae*)
C. integriloba Sarg.	(*succulenta* × *punctata*)	(*Macracanthae* × *Punctatae*)
C. ardua Sarg.	(*succulenta* × *punctata*)	(*Macracanthae* × *Punctatae*)
C. divida Sarg.	(*succulenta* × unspecified)	(*Macracanthae* × *Brainerdianae*)
C. chadsfordiana Sarg.	(unspecified × unspecified)	(*Macracanthae* × *Pruinosae*)
C. putata Sarg.	(unspecified × unspecified)	(*Macracanthae* × *Pruinosae*)
C. laurentiana Sarg.	(*succulenta* × *brunetiana*)	(*Macracanthae* × *Rotundifoliae*)
**C. simulata* Sarg.	(*calpodendron* × *palmeri*)	(*Macracanthae* × *Crus-galli*)
**C. nuda* Sarg.	(*succulenta* × *crus-galli*)	(*Macracanthae* × *Crus-galli*)
**C. vailiae* Britton	(*calpodendron* × *uniflora*)	(*Macracanthae* × *Parvifoliae*)

season of six to eight weeks separating *C. mollis* (Torr. & A. Gray) Scheele (early) and *C. phaenopyrum* (L.f.) Medik. (late) when sympatric, the anthesis of the other species ranged between, it is obvious that the number of species pairs of similar anthesis phenology is lower than the number of sympatric pairs, yet sympatric pairs are calculated on the basis of all taxa occurring in the state. Correction for sufficiently similar anthesis phenology and local sympatry would undoubtedly raise the F value calculated; however, the scale of work necessary to accumulate such information would be large. The value F, therefore, only generates a particular estimate of hybridization. What is most secure about these findings is that the putative hybrids are all wide and all extinct or rare.

There are no grounds for directly extrapolating the frequency of interserial hybrids in Missouri to larger regions of the continent as a whole, because of the effects of different species lists and the dif-

Table 2. Additional putative hybrids of *Crataegus* for the northeastern United States and Canada in Gleason and Cronquist (1991).

Name of taxon	Presumed parental species acc. to E.J.P.	Parental series
C. anomala Sarg.	(*coccinea* × *mollis*)	(*Coccineae* × *Molles*)
C. apiomorpha Sarg.	(*coccinea* × *flabellata*)	(*Coccineae* × *Tenuifoliae*)
C. harryi Sarg.	(*brainerdii* × *punctata*)	(*Brainerdianae* × *Punctatae*)
C. idea Sarg.	(*brainerdii* × *rotundifolia*)	(*Brainerdianae* × *Rotundifoliae*)
C. improvisa Sarg.	(*brainerdii* × *coccinea*)	(*Brainerdianae* × *Coccineae*)
C. kennedyi Sarg.	(*brainerdii* × *pruinosa*)	(*Brainerdianae* × *Pruinosae*)
C. knieskerniana Sarg.	(*coccinea* × *flabellata*)	(*Coccineae* × *Tenuifoliae*)
C. laetifica Sarg.	(*crus-galli* × *succulenta*)	(*Crus-galli* × *Macracanthae*)
C. laneyi Sarg.	(*brainerdii* × *succulenta*)	(*Brainerdianae* × *Macracanthae*)
C. lecta Sarg.	(*brainerdii* × *succulenta*)	(*Brainerdianae* × *Macracanthae*)
C. mansfieldensis Sarg.	(*coccinea* × *punctata*)	(*Coccineae* × *Punctatae*)
C. membranacea Sarg.	(*pruinosa* × *succulenta*)	(*Pruinoseae* × *Macracanthae*)
C. menandiana Sarg.	(*punctata* × *succulenta*)	(*Punctatae* × *Macracanthae*)
C. neobaxteri Sarg.	(*punctata* × *rotundifolia*)	(*Punctatae* × *Rotundifoliae*)
C. pausiaca Sarg.	(*crus-galli* × *punctata*)	(*Crus-galli* × *Punctatae*)
C. puberis Sarg.	(*flabellata* × *punctata*)	(*Tenuifoliae* × *Punctatae*)
C. randiana Sarg.	(*brainerdii* × *flabellata*)	(*Brainerdianae* × *Tenuifoliae*)
C. rotundata Sarg.	(*pruinosa* × *rotundifolia*)	(*Pruinosae* × *Rotundifoliae*)
C. rubrocarnea Sarg.	(*brainerdii* × *flabellata*)	(*Brainerdianae* × *Tenuifoliae*)
C. shirleyensis Sarg.	(*brainerdii* × *punctata*)	(*Brainerdianae* × *Punctatae*)
C. spatiosa Sarg.	(*pruinosa* × *succulenta*)	(*Pruinosae* × *Macracanthae*)
C. websteri Sarg.	(*brainerdii* × *calpodendron*)	(*Brainerdianae* × *Macracanthae*)
C. whittakeri Sarg.	(*calpodendron* × *mollis*)	(*Macracanthae* × *Molles*)

ferent degrees of sympatry that exist. Also, for northeastern North America, the 65 putative hybrid names do not reflect the degree of attention that has been given to Missouri *Crataegus*, and a methodical scrutiny of the relevant basionyms may well turn up more. In the northeastern United States and adjacent Canada, where 65 species are suggested as hybrid (Tables 1, 2), this is in the context of about 850 species names for the same area (Palmer, 1925). This generates a lower percentage (7.6%) than for Missouri (15%). However, calculating the percentage of all interserial hybrids (i.e., counting as the same nothospecies situations where the parents belong to the same series but where the hybrids have different binomials) as a fraction of all possible interserial cases, i.e., where $x = 35$ (Table 6) and $n = 18$ (Palmer in Gleason, 1952), F = 22.8%, about a third more than for the Missouri data alone. Presumably the co-existence of parental species over a much larger area than the state of Missouri inflates the total. As with Missouri, the new putative interserial hybrids placed

Table 3. Additional putative interserial hybrids of *Crataegus* found in Missouri suggested in this paper.

Name of taxon	Presumed parental species acc. to E.J.P.	Parental series
C. atrorubens Ashe	(? *mollis* × ? *viridis*)	(? *Molles* × ? *Virides*)
C. dawsoniana Sarg.	(? × *viridis*, s.l.)	(? × *Virides*)
C. dispessa Ashe	(*collina* × *mollis*)	(*Punctatae* × *Molles*)
C. glabrifolia Sarg.	(*pruinosa* × *margaretta*)	(*Pruinosae* × *Rotundifoliae*)
C. harveyana Sarg.	(? *intricata* × *calpodendron*)	(? *Intricatae* × *Macracanthae*)
C. intermixta Sarg.	(*crus-galli*, s.l. × *viridis*, s.l.)	(*Crus-galli* × *Virides*)
C. lawrencensis Sarg.	(*crus-galli*, s.l. × *viridis*, s.l.)	(*Crus-galli* × *Virides*)
C. lettermanii Sarg.	(*margaretta* × *collina*)	(*Rotundifoliae* × *Punctatae*)
C. nitens (?) Sarg.	(*viridis*, s.l. × ? *pruinosa*)	(*Virides* × ?*Pruinosae*)
C. noelensis Sarg.	(*collina* × *mollis*)	(*Punctatae* × *Molles*)
C. pudens Sarg.	(*crus-galli*, s.l × ?)	(*Crus-galli* × ?)
C. sicca Sarg.	(*pruinosa* × *margaretta*)	(*Pruinosae* × *Rotundifoliae*)
C. verruculosa Sarg.	(? × *crus-galli*, s.l.)	(*Punctatae* × *Crus-galli*)

Table 4. List of accepted orthospecies of Missouri *Crataegus*.

I.	ser. *Apiifoliae*
	1. *C. marshallii* Eggl.
II.	ser. *Microcarpae*
	2. *C. spathulata* Michx.
III.	ser. *Cordatae*
	3. *C. phaenopyrum* (L.f.) Medik.
IV.	ser. *Virides*
	4. *C. viridis* L.
	5. *C. nitida* (Engelm.) Sarg.
V.	ser. *Crus-galli*
	6. *C. reverchonii* Sarg.
	7. *C. crus-galli* L.
	8. *C. berberifolia* Torr. & A. Gray
	9. *C. fecunda* Sarg.
VI.	ser. *Punctatae*
	10. *C. collina* Chapm.
	11. C. spes-aestatum J. B. Phipps, ined.
VII.	ser. *Rotundifoliae*
	12. *C. margaretta* Ashe
VIII.	ser. *Pruinosae*
	13. *C. pruinosa* (H. L. Wendl.) K. Koch
	14. *C. dissona* Sarg.
	15. *C. gattingeri* Ashe
IX.	ser. *Intricatae*
	16. *C. biltmoreana* Beadle
	17. *C. neobushii*
	18. *C. ? intricata* Lange
	19. *C. padifolia* Sarg.
X.	ser. *Tenuifoliae*
	20. *C.* sp. cf. *macrosperma* Ashe
XI.	ser. *Macracanthae*
	21. *C. calpodendron* (Ehrh.) Medik.
	22. *C. macracantha* Lodd.
XII.	ser. *Dilatatae*
	23. *C. coccinioides* Ashe
XIII.	ser. *Molles*
	24. *C. mollis* (Torr. & A. Gray) Scheele
	25. *C. texana* Buckley
XIV.	ser. *Parvifoliae*
	26. *C. uniflora* Münchh.

into the equation for the northeastern United States and adjacent Canada all appear to be rare or extinct, although for this large area detailed and accurate modern knowledge is only sporadic. If this is an accurate interpretation, then taxonomic problems deriving from fairly wide hybridization in North American hawthorns subsist mainly in the number of putative hybrid situations that have to be taken into account, i.e., perhaps 15%–20% of the synonymy, rather than in the likelihood, which appears to be extremely low, that any given specimen encountered is hybrid. Extension of an analysis of this kind to larger geographical areas has little point due to the lack of sympatry of so many taxa.

Implications of Degree of Taxonomic Relatedness

I will now consider some taxonomic aspects of interserial hybridization in Missouri. Figure 1 indicates that only three monotypic and certainly taxonomically isolated series in Missouri are without putative interserial hybrids in the state. Thus, *Crataegus phaenopyrum* (ser. *Cordatae* Beadle ex Eggl.) Rehder) has no recorded hybrids with other *Crataegus* species in Missouri, or indeed anywhere, though whether this is due to taxonomic isolation or just the very late relative anthesis phenology is not clear. When sympatric (including cultivated sympatry), *C. phaenopyrum* begins to flower just after the second-last species in the sequence (*C. calpodendron* (Ehrh.) Medik.) finishes flowering. This may be as late as early June in east-central Missouri (pers. obs.). On the other hand, *C. spathulata* Michx. (ser. *Microcarpae* (Loudon) Rehder), a generally common southeastern United States species, is also never a suggested parent of a hybrid, even though it has mid-spring anthesis phenology when many other sympatric species of *Crataegus* are flowering, and therefore in this case it is probably its taxonomic isolation that is significant. Another taxonomically isolated Missouri *Crataegus*, *C. marshallii* Eggl. (ser. *Apiifoliae* (Loudon) Rehder), is as well a widespread and common species outside of Missouri, and also of early to mid-season anthesis phenology when many other sympatric *Crataegus* are flowering. It, too, is without putative hybrids in the state, though there do exist two plausible examples. These are *C.* ×*notha* Sarg. (presumptively × *C. mollis* (Torr. & A. Gray) Scheele), and *C. lacera* Sarg., both, however, from Arkansas and both very rare. Possible hybridity for *C. notha* was first suggested by Sargent (1921) and for *C. lacera* is proposed in this paper. If, indeed, the difficulty of making hybrids within *Crataegus* generally increases with taxonomic isolation, as it commonly does in other taxa, then this is a further factor of interest with regard to interserial hybridization.

In Missouri, the putative hybrids apparently readily found by Crataegophiles during the heyday of hawthorn discovery, ca. 1890–1930, are nearly all vanished, only *C.* ×*vailiae* Britton and *C.* ×*sicca* Sarg. certainly persisting according to herbarium records at MO. It needs underlining that this was when *Crataegus* was certainly far more abundant in Missouri than today and not merely a period of greater collection activity. Not only, therefore, was

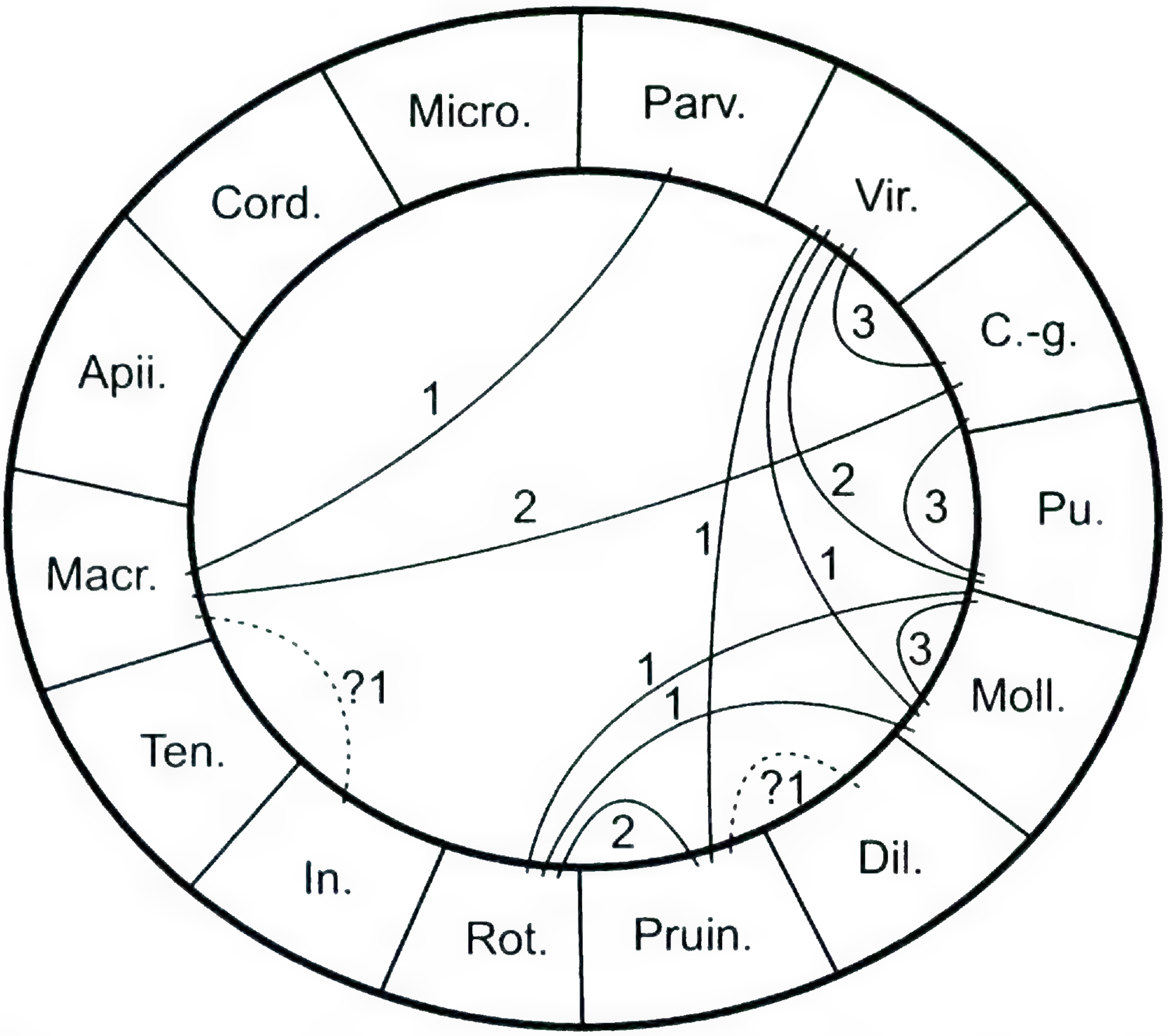

Figure 1. Diagram indicating frequency of putative hybrids in Missouri *Crataegus*. Abbreviations in outer circle indicate parental taxa by series. Connecting lines indicate putative hybrids; if dotted, questionable. Numbers indicate number of named entities found in Missouri. Abbreviations are: (Apii)foliae, (Cord)atae, (C)rus-(g)alli, (Dil)atatae, (In)tricatae, (Macr)acanthae, (Micro)carpae, (Moll)es, (Parv)ifoliae, (Pruin)osae, (Pu)nctatae, (Rot)undifoliae, (Ten)uifoliae, (Vir)ides.

Table 5. Putative interserial hybrids of *Crataegus* in Missouri grouped by name of parental series.

Crus-galli × *Macracanthae*
  C. nuda, C. simulata
Crus-galli × *Punctatae*
  C. collicola, C. pudens, C. verruculosa
Crus-galli × *Virides*
  C. danielsii, C. intermixta, C. lawrencensis*
Crus-galli × unknown
  C. verruculosa
Intricatae × *Macracanthae*
  C. harveyana
Macracanthae × *Parvifoliae*
  C. vailiae
Macracanthae × *Punctatae*
  C. incaedua
Molles × *Pruinosae*
  C. locuples
Molles × *Punctatae*
  C. noelensis, C. dispessa, C. latebrosa
Molles × *Rotundifoliae*
  C. kellogii
? *Molles* × ? *Virides*
  C. atrorubens
Pruinosae × *Virides*
  C. nitens
Punctatae × *Rotundifoliae*
  C. lettermanii
Punctatae × *Virides*
  ?C. dawsoniana
Virides × unknown
  C. dawsoniana

* *Crus-galli* × *Punctatae* according to E. J. Palmer.

Table 6. Series pairs generating at least one interserial hybrid in area of Palmer in Gleason (1952).

Brainerdianae × *Dilatatae*	*Macracanthae* × *Molles*
Brainerdianae × *Macracanthae*	*Macracanthae* × *Parvifoliae*
Brainerdianae × *Pruinosae*	*Macracanthae* × *Pruinosae*
Brainerdianae × *Punctatae*	*Macracanthae* × *Punctatae*
Brainerdianae × *Rotundifoliae*	*Macracanthae* × *Rotundifoliae*
Brainerdianae × *Silvicolae*	*Molles* × *Pruinosae*
Brainerdianae × *Tenuifoliae*	*Molles* × *Punctatae*
Coccineae × *Brainerdianae*	*Molles* × *Rotundifoliae*
Coccineae × *Dilatatae*	*Molles* × *Virides*
Coccineae × *Molles*	*Pruinosae* × *Punctatae*
Coccineae × *Punctatae*	*Pruinosae* × *Rotundifoliae*
Coccineae × *Silvicolae*	*Pruinosae* × *Silvicolae*
Coccineae × *Tenuifoliae*	*Pruinosae* × *Tenuifoliae*
Crus-galli × *Macracanthae*	*Pruinosae* × *Virides*
Crus-galli × *Punctatae*	*Punctatae* × *Rotundifoliae*
Crus-galli × *Virides*	*Punctatae* × *Tenuifoliae*
Intricatae × *Macracanthae*	*Punctatae* × *Virides*
Intricatae × *Pruinosae*	

Series without hybrids in this floristic region—*Apiifoliae*, *Cordatae*, *Douglasianae*, *Microcarpae*.

the potential for hybridization proportionately greater, but other recognizable and unusual forms, today subsumed in the wider context of various orthospecies, were collected which also can no longer be found. The overall conclusion, therefore, from the Missouri data, is that among sympatric *Crataegus* species of similar anthesis phenology, and belonging to different series, whereas there appears to have been extensive opportunity for the creation of hybrid hawthorns, it does not appear to have been plentifully materialized. Indeed the hybrids, though fairly numerous by name are nearly all extinct and were never common. Even the persisting *C.* ×*sicca* and *C.* ×*vailiae* are rare. It is thus abundantly clear that wide hybrids in North America, at least as we recognize them, do not constitute either a significant taxonomic problem nor, probably, a significant evolutionary conduit.

In Europe, by contrast, the situation is very different, and calculation of my F from information in Christensen's (1992) monograph yields a value of 80%, with *C. monogyna* being a parent three times as frequently as the next species, the regionally abundant *C. laevigata* (Poir.) DC., *C. microphylla* C. Koch, and *C. rhipidophylla* Gand. While this may in part be a product of European *Crataegus* having received more attention than North American *Crataegus*, it is possibly also related to the high frequency of 20-stamen sexual diploids in Europe, where no 10-stamen species are known, an issue that received interesting attention with respect to some of the North American black-fruited hawthorns in Dickinson et al. (1996). In my view, although the jury is still out on this issue, I am comfortable accepting empirically different findings for different clades within *Crataegus*.

Table 7. Summarized reproductive data of putative parental species of putative hybrids of *Crataegus* in Missouri. Sx = sexual, ap = apomictic (all non-MO data).

Name	Series	Ploidy	# of hybrids generated	Breeding systems	# of distinct putative hybrids
C. calpodendron	*Macracanthae*	2*x*	4	sx	4
C. collina	*Punctatae*	—	7	—	4
C. crus-galli	*Crus-galli*	3*x*, 4*x*	7	sx, ap	2
C. margaretta	*Rotundifoliae*	—	4	—	3
C. mollis	*Molles*	2*x*	4	sx	3
C. noelensis	*Molles* ?	—	1	—	1
C. pruinosa	*Pruinosae*	3*x*, 4*x*	4	sx, ap	2
C. succulenta	*Macracanthae*	3*x*	1	ap	1
C. uniflora	*Parvifoliae*	—	1	—	1
C. viridis	*Virides*	—	5	—	3

Development of Views on North American *Crataegus* Hybridization

Most early workers such as Sargent believed in the validity of the many species described (Brown, 1910). Thus, with Sargent (Macklin et al., 2002) only two intermediate situations were touted among the 732 he described. These are *Crataegus notha*, described as intermediate between *C. mollis* and *C. marshallii* by Sargent (1921), who said that if it were a hybrid it would be the only one known in North America, and *C. intermixta* (Sargent, 1922), where he indirectly suggested intermediacy. *Crataegus notha* appears to be the first specific instance of potential hybridization in North American *Crataegus* alluded to by anyone. It should be noted that Sargent's belief in non-hybridization of *Crataegus* was rooted in their ability to breed true, based on the large seed-originated collections at his workplace, the Arnold Arboretum. The lack of variation in the numerous seedling varieties grown in Jamaica Plain does lend support, however, to the principal thesis of this paper, one of rarity of hybrids.

Ashe, Beadle, Brainerd, and Dunbar (quoted in Brown, 1910) all held that *Crataegus* could hybridize, but very little substantiation of this position is given by them. Eggleston also presented the same position, though less clearly, in Brown (1910), even though two years earlier he (Eggleston, 1908: 74) had explicitly suggested that "much of the (taxonomic) trouble found in *Crataegus* arises from hybridization." There is no critical elaboration of this statement anywhere in Eggleston's writings, and in practice the idea seems to have been ignored by him. Palmer's *Crataegus* publications began with his significant nomenclator (Palmer, 1925), which gathered together and organized the over 1200 North American species of *Crataegus* so far described. Belief in the distinctness of so many species was perhaps already suspended, but hybrid possibilities were, nevertheless, not mentioned. Palmer became influenced by the biosystematic school then developing, and in his seminal paper "The *Crataegus* problem" (Palmer, 1932) he suggested that some of the variation present might have been derived from hybridization, but that most had been formed by the normal processes of evolution, which we can understand as meaning adaptive radiation. In this view of hybridization frequency Palmer was close to those authors already quoted by Brown (1910), who had alluded to possible *Crataegus* hybridization but did not document it. Rickett's (1936, 1937) papers on the fine-scale variation in Missouri *Crataegus* quote Palmer's becoming-classic phrase "The *Crataegus* Problem" and the second one makes considerable reference to hybridization, especially instancing an interserial hybrid, *C. danielsii* E. J. Palmer. On the other hand, the biosystematist Camp's widely cited 1942 paper dwells on apomixis and polyploidy as creating "The *Crataegus* Problem" but does not implicate hybridization. By the 1940s, Palmer (1943: 374), discussing the species concept in *Crataegus*, said that most species were as readily distinguishable as those in other equally speciose genera and that "many species growing together do not hybridize in nature . . . and it is probable that hybrids are no more common relatively in *Crataegus* than in many other genera." Later, Palmer (1946: 472) made the slightly different statement that hybridization was a factor to be reckoned with in *Crataegus* taxonomy but did not expand on the suggestion. Only after the passage of a quarter of a century since his first *Crataegus* paper had Palmer (1952) come to specific grips with the hybridization issue, and there he finally noted many putative hybrids (Table 1). Further examples were suggested by Cronquist (see Table 2), who penned the treatment for Gleason and Cronquist (1963). Kruschke (1965), by contrast, who had rather typological taxonomic views, did not indicate any hybrids. We may compare this with Van Valen (1976), viewing *Crataegus* from the perspective of "ecological species" and "multispecies," who famously averred that there may be no species in *Crataegus*. Finally, there is my own work on *Crataegus*, developed over the last 25 years or so. My earlier position took up the then-current paradigm that apomixis, hybridization, and polyploidy shared responsibility for the *Crataegus* problem (e.g., Phipps & Muniyamma, 1980), although the paucity of documentation for hybridization was explicitly noted. Eventually (this paper), I propose a few more examples of hybridization (Table 3). It has taken this length of time to jettison the received outlook that hybridization in North American *Crataegus* is frequent, and my latest position is that wide hybridization does not seem to be a significant factor causing the taxonomic difficulties so prevalent in North American *Crataegus*.

Several conclusions stem from this historical review. First, as might be expected, there was only a gradual development of the idea that hybridization is a significant element in *Crataegus* taxonomy. Second, crystallization of the originally somewhat inchoate positions on hybridization only happened when actual cases were adduced in a sufficiently convincing way. Third, this crystallization was effected almost in its entirety by persons working in a floristic mode. It is also interesting to note that

none of the more recent workers who seek to radically reduce the number of *Crataegus* species, most strikingly Little (1979) and Cronquist (1963; Gleason & Cronquist, 1991), is a person who has ever made specific studies on *Crataegus* taxonomy.

Observations on Hybrid Frequency and the Reproductive Biology of *Crataegus*

The quantitative significance of interserial hybrid frequency lies not merely in the proportion of all possible crosses represented, but in their abundance on the ground as well as their ability to perpetuate, the biological significance being either as vectors for gene flow or as the beginnings of new taxa. As well, likelihood of occurrence as such constitutes a broad measure of affinity, and it may be helpful to review what is known about hybridization in those genera most closely related to *Crataegus*, specifically, therefore, in Rosaceae subfam. Maloideae.

Subfamily Maloideae of the Rosaceae is notorious for the number of cases of intergeneric hybridization, both in wild situations and in cultivation. Fifteen intergeneric hybrid pairs are known (Robertson et al., 1991), some from more than one parental species. In spite of this, only two intergeneric combinations are moderately frequently encountered in the world as a whole, these being *Sorbus* × *Torminaria* and *Sorbus* × *Aria*, both of which have a number of nothospecies that persist in the wild, some of them moderately common, for instance *Sorbus mougeotii* Soyer-Willemet & Godron (*Sorbus* × *Torminaria*) and *S. latifolia* (Lam.) Pers. (*Sorbus* × *Aria*). Partly as a consequence of the maloidean situation, therefore, the presumed existence of abundant hybridization in *Crataegus* has so far evoked little critical comment. However, one should not over-emphasize the maloideae data. While superficially it appears as if subfamily Maloideae in general may be particularly prone to wide hybridization, the fact is that this is limited to certain species in particular genera, and many of the intergeneric hybrids reported are scarce. Eight maloid genera that are substantially sympatric with others report no intergeneric hybrids, though intergeneric hybrids are quite common between some members of *Aria* and *Sorbus*. But even within these two genera hybridization is restricted to hybrids with *S. aucuparia* L. in Europe, with no such reported cases in the speciose, sympatric parts of those genera in Asia beyond the range of *S. aucuparia*. *Sorbus aucuparia* may therefore have something in common with *Crataegus monogyna*.

Maloideae mostly flower in the spring and are often sympatric, when many species flower synchronously. Hawthorns are mainly mass-flowering, herkogamous plants with unspecialized pollinator systems (Power, 1980; Dickinson, 1985). However, because of this pollination system and the fairly numerous species of *Crataegus* that are both sympatric and flower more or less synchronously, they must inevitably cross pollinate in some species pairs with some frequency. Nevertheless, where the basic taxonomy is understood, the great majority of hawthorn plants encountered in the field appear to be non-hybrid. In the case of *Crataegus punctata*, for instance, a common sexual diploid of the northeastern quarter of the United States and adjacent Canada, the ratio of pure *C. punctata*, determined on a morphological basis, to putative *C. punctata* hybrids determined on a morphological basis, must be at least 10,000:1 (author, pers. obs.). A parallel observation has been made by Palmer (1943, 1946), and to my knowledge this position is quite clear to all who work with *Crataegus*. Discussion with other major fieldworkers on *Crataegus*, for instance, Welby Smith (pers. comm.) of Minnesota, who has collected upward of 800 *Crataegus* specimens in that state in recent years for his "Woody Plants of Minnesota" (W. Smith, in prep.), is in complete agreement with this position. Thus, recognized hybrids or putative hybrids in North American *Crataegus* seem to be extremely uncommon on the ground and there is, therefore, presumably some barrier to the formation of fertile hybrids.

It is a commonplace of evolutionary biology that adaptive radiation has to be coupled with barriers to crossing to protect the integrity of the descendent gene pools, and thus their adaptability to their new niches. It may be presumed that an even stronger effect occurs with intergeneric pollination, and this is no doubt relevant to the situation in the wider subfamily. Nevertheless, to my knowledge, no one has discovered the mechanism that prevents the almost certainly frequent cross pollination between *Crataegus* species from yielding so few hybrid offspring. The general causes of relevant barriers to gene flow are pre- and post-zygotic isolating mechanisms, which I will now discuss briefly below.

Assuming no barrier to cross pollination between sympatric species with similar anthesis phenology, other than degree of contiguity of the individual bushes, the most likely pre-zygotic mechanism to prevent cross fertilization has to be connected with competition between self species and non-self species pollen. Although not demonstrated for *Crataegus*, this has been well established for *Salix* (Moeseler, 1989, 1990). Indeed, if the same mechanism exists in *Crataegus* then isolated bushes of self-

incompatible species, not a particularly unusual situation in my experience, could be ideal vehicles for producing hybrids. It may be presumed, based on limited evidence from elsewhere in North America (Muniyamma & Phipps, 1985), that *C. mollis*, parent of three or four Missouri putative hybrids, may be a self-incompatible diploid while *C. calpodendron*, parent of two putative hybrids in Missouri, may be a facultatively apomictic diploid (Muniyamma & Phipps, 1984). *Crataegus crus-galli*, parent of seven Missouri putative hybrids, is either a triploid or tetraploid, apomict or facultative inbreeder outside Missouri (Dickinson & Phipps, 1986), while *C. pruinosa*, parent of four putative Missouri hybrids, is an apomictic triploid in Ontario (Muniyamma & Phipps, 1984). Comparable information on the other five putative parental species for Missouri is lacking. Clearly, this scant information does not support the pollen competition theory, hybrid taxa occurring at least as frequently in self-compatible taxa. The other side of this coin is that the relatively high frequency of presumed self-incompatible common diploids is coupled with the low to very low abundance of fairly wide hybrids, and this also appears to suggest that pollen competition may not be the normal *Crataegus* scenario. Unfortunately, the ploidy level and breeding system of *Crataegus* taxa provide no published instate data and some of the examples quoted above are based on tiny samples. Even taking into account the totality of the geographical range of putative parents, only a few chromosome counts and very little breeding data is available (Table 7), and none for the putative hybrids. Reproductive data for *C. collina*, parent of seven hybrids, do not exist. *Crataegus succulenta* Schrad. ex Link, an apomictic triploid in Ontario (Muniyamma & Phipps, 1984), is the putative parent of one Missouri hybrid, although perhaps the correct interpretation of the putative parent is *C. macracantha*, which would be a self-compatible sexual species and/or apomict.

When we consider post-zygotic mechanisms of limiting gene flow, then immediate developmental problems at the zygote or embryo level could significantly reduce both parental fitness and also sterility of the mature F_1 generation, due to meiotic irregularities, including the obvious case of triploidy, would prevent reproductive success of the F_1. This, therefore, appears the most likely cause of hybrid rarity for North American *Crataegus*. A subordinate question thus arises: is hybrid rarity due to a poor ability to generate hybrids or to the poor ability of hybrids to perpetuate themselves? Perhaps both explanations are true.

Because this paper deals with hybrids, the issue of possible apomixis in parents seems to have little relevance. The putative hybrids noticed must be generated sexually except in the rare cases of production of unreduced gametes. The issue of rarity (actually, in most cases now, extinction) of the putative hybrids also explains why there is no data on their reproductive behavior. There is, however, no *a priori* reason why the known putative hybrids should not be at least adequately fitted to their habitats since from the little data available, mature plants of putative hybrids that have yielded herbarium specimens are as flourishing as other adjacent non-hybrid individuals. It is, therefore, most likely that the putative hybrids identified are, firstly, sexual and, secondly, have meiotic problems. In addition, if hybrid but sterile seed is set in significant quantity, this lowers the fitness of the hybrid parents and detrimentally affects their success. This aspect has also not been investigated in *Crataegus* to date, so further comment is redundant. There is still so little hard data about the breeding systems and chromosome number of most North American *Crataegus* species that further speculation along these lines does not seem fruitful at this stage. But it does suggest an important avenue for research.

Consequences for Floras

Problems with *Crataegus* identification render much of *Crataegus* taxonomically almost intractable for many workers, including otherwise excellent systematists whose main interests lie elsewhere. One component of this is that hybrids add to the key burden (see Osborne, 1963, on factors affecting the possibility of correct identification). Hybrids in any genus are usually particularly difficult to key out since the normal bifurcation in keys mimics evolutionary radiation, and hybrids need reticulation or trifurcation in keys, both of which create problems in construction and use, not to mention editorial dislike of trifurcation. The perhaps 20% of North American *Crataegus* taxa that are interserial hybrids therefore constitute a significant burden on the key. This can be mitigated by deleting hybrids from keys and also by clearly noting the low abundance and sporadic occurrence (if true, as it usually is) of putative hybrids in *Crataegus* in the descriptive text so as to clearly differentiate them from the more widely occurring orthospecies. This is perhaps particularly important in state and local floras, where it can be assumed that relatively detailed abundance of data exists. However, this is not sufficiently often done, and the identifier is therefore confronted with serious problems of rec-

ognizing these situations. Flagging the more or less rare putative hybrids and deleting them from keys would constitute two important improvements.

Conclusions

Interserial hybridization in North American *Crataegus* is estimated to have been historically about 14% of all possible Missouri cases and 20% of all possible northeastern United States cases, but the numbers of hybrid individuals on the ground appear to be low to very low at best and perhaps, more commonly at this time, non-existent. The frequency and persistence of hybridization appear to be, at least approximately, reflective of the taxonomic/genetic distance between species. If so, the taxonomic situation in North American *Crataegus* combines the following elements: first, a suite of genetically, phenologically or occasionally geographically, more or less isolated species nearly or completely without natural hybrids, e.g., *C. spathulata*; second, a further suite of at least reasonably distinct (i.e., in different series) taxa, e.g., *C. collina* and *C. viridis*, between which there occur rare and mainly non-persistent hybrids; third, species complexes undergoing vigorous raciation without hybridization; and conceivably, fourth, a possibly large group of intraserial hybrids superimposed on species complexes undergoing vigorous raciation. This fourth group, of course, cannot at present be distinguished from the third and includes at least *C. crusgalli* and *C. pruinosa*, both sensu lato. I believe that it is these last two situations, which are presently manifest to our minds as a series of extraordinarily polymorphic species, or species complexes, treated by different workers at different taxonomic ranks and wherein, by strict definition, hybridization could not exist, that constitutes the real taxonomic challenge at the species level (Camp's "veritable witches' brew") of North American *Crataegus*.

The question remains, therefore, whether the relatively low frequency of wide hybridization in North American *Crataegus*, both putative and documented, is an artifact of poverty of study, or whether it is real. In my view, although only slowly and asymptotically coming to full resolution, there have already been enough tenacious and perspicacious workers on North American *Crataegus* to uncover a high proportion of wide hybrids. If this is set in the context of very variable hybridization rates in different parts of subfamily Maloideae as a whole, apparently mirrored in *Crataegus* according to current understanding, this is an important and perfectly plausible finding differentiating the main North American clade of *Crataegus* from the main western Eurasian (sect. *Crataegus*) clade as well as making similar distinction among groups of North American *Crataegus* species. This is particularly the case in view of the fact that two-thirds of the documented examples of hybridization in North America involve the European *C. monogyna*.

It is clear, therefore, that suggestions of widespread hybridization as a cause of taxonomic confusion in North American *Crataegus* are not valid, insofar as known and putative hybrids are concerned. This does not invalidate, however, a different, feasible but substantial hypothesis that there might be widespread and undetected hybridization between closely similar entities within the genus.

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POLLINATION BIOLOGY OF FOUR *PEDICULARIS* SPECIES (SCROPHULARIACEAE) IN NORTHWESTERN YUNNAN, CHINA[1]

Hong Wang[2] *and De-Zhu Li*[2]*

ABSTRACT

Pedicularis L. (Scrophulariaceae) represents a classic example of floral morphological diversity for pollination biologists. In the species-rich areas of the Himalayas there have been few studies on the pollination syndromes of *Pedicularis*, especially of the long-tubed species. In the summer and fall of 2000, the pollination biology of four species of *Pedicularis* was studied in Zhongdian of northwestern Yunnan, China. The four species, foraged by three bumblebee species, possess two different corolla types: *Pedicularis lutescens* Franch. ex Maxim. subsp. *lutescens* and *P. densispica* Franch. ex Maxim. have a short-tubed, erostrate, and nectariferous corolla type and are pollinated exclusively by *Bombus friseanus* Skorikov and *B. lucorum* Latr. workers foraging flower nectar and pollinating nototribically; *P. integrifolia* Hook. f. and *P. tricolor* Hand.-Mazz. have long-tubed, rostrate, and nectarless corollas and are pollinated sternotribically by *Bombus festivus* Smith and *B. friseanus* workers hanging on the S-shaped beak or supported by the bowl-shaped lower lips. Cross-pollination by bumblebee workers is the most important reproductive mechanism observed for these *Pedicularis* in Yunnan. Nectar-foraging bumblebee queens and lepidopteran moths or butterflies were not found to pollinate any of these *Pedicularis* species. Otherwise, the interactions between *Pedicularis* and *Bombus* and pollination mechanisms in northwestern Yunnan are similar to those in Japan and North America. The present study provides new evidence that the Japanese species had evolved from Himalayan migrants in a pattern parallel to that of North American species.

Key words: *Bombus*, northwestern Yunnan, *Pedicularis*, pollen/ovule ratio, pollination mechanism, Scrophulariaceae.

Pedicularis (Scrophulariaceae) comprises some 600 to 800 species (Wang et al., 2003) and is one of the largest angiosperm genera in the Northern Hemisphere (Mabberley, 1987; Yang et al., 1998). The species of *Pedicularis* are generally perennial or annual (rarely biennial) herbs hemiparasitic on grasses. Floral morphology displays striking differences in the corolla shape and the length of the corolla tube. The corolla is strongly zygomorphic, consisting of an upper lip (galea) enclosing four introrse anthers and a style running the length of the galea, with the stigma exserted beyond its tip. The galea can be variously beaked, toothed, and crested, while the lower lip is variously trilobed, usually spreading, and external to the upper lip in bud. Of four general corolla forms in the genus described by Maximowicz (1888) and Li (1951)—i.e., beakless, toothless; beakless, toothed; beaked, short-tubed; beaked, long-tubed—only the last is absent from Japan and North America, and this corolla form appears in species endemic to the Himalayas (Macior, 1984). Because of its diverse corolla forms and large number of species, the origin and evolution of *Pedicularis* have long intrigued botanists. Limpricht (1924) considered the Himalayan region as a center of origin, although Prain (1890) earlier suggested that *Pedicularis* originated in the Holarctic and dispersed from a common boreal center. Hong (1983) identified a small area in the Himalayas, in western Sichuan and northwestern Yunnan, as containing ca. 300 species of *Pedicularis*. Pointing out the morphological diversity and high degree of endemism in this region, Macior (1982, 1988) also favored the Himalayan origin hypothesis.

Pedicularis displays enormous diversity of floral form (Pennell, 1948) and is a classic example of pollination syndrome diversification within a genus. Beginning in the late 19th century, pollination mechanisms of *Pedicularis* have been studied in

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[2] Laboratory for Plant Biodiversity and Biogeography, Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, Yunnan 650204, China. *Author for correspondence: dzl@mail.kib.ac.cn.

North America and Europe. Müller (1881), Weed (1884), and Kunth (1898–1905) primarily considered the floral morphology and the foraging behaviors of the pollinators. Since then, Macior (see 1982 for a summary of earlier studies; Macior, 1984, 1986) made a systematic and thorough investigation of the pollination ecology, endemic adaptation, and evolution of pollination mechanisms in *Pedicularis*, primarily in the North American species. Meanwhile, Sprague (1962), Faegri and van der Pijl (1966), MacInnes (1972), and Kwak (1979) demonstrated similar patterns of pollination ecology in this genus as well as co-adaptations between *Pedicularis* and its pollinators. Earlier studies revealed that the evolution of *Pedicularis* has been closely co-adapted to its pollinators, principally bumblebees (*Bombus*). Pollination has been noted for a solitary bee (*Osmia tristella*) in *P. semibarbata* L. (Macior, 1977) and by hummingbirds in *P. densiflora* Benth. (Macior, 1986), with these seen as more recent adaptations. Such phenomena have not yet been observed in Chinese *Pedicularis*, but there are hundreds more taxa to observe. The pollination ecology of *Pedicularis* in Asia remained completely unknown until Macior (1988) made his first study in Japan. Interestingly, his Japanese observations revealed a close parallel between pollination mechanisms in Japan and North America. Subsequently, some Asian species were observed primarily from the western and Chinese Himalayas (Macior, 1991; Macior & Sood, 1990, Macior & Tang, 1997, 1999; Wang & Li, 1998; Macior et al., 2001). This study was extended to the Himalayan species, especially those bearing flowers of the unique long-tubed corolla type, found only in the Himalayas. It was suggested that the species with long-tubed beaks were adapted to moth pollination (Pennell, 1943). However, Macior's preliminary observations revealed that the long, nectarless corolla tube was probably a floral adaptation of these plants, which are dwarf-sized at high elevations, for attracting other pollinators. Obviously, more case studies are needed to test Pennell's hypothesis and to compare Macior's results in Japan and the western Himalayas. There are 352 species of *Pedicularis* in China, of which some 272 species are endemic (Yang et al., 1998), with some transboreal species of extensive geographic disjunctions (Macior, 1988), e.g., *P. verticillata* L. In southwestern China, the province of Yunnan contains 151 species of *Pedicularis*, including all four corolla forms, with about half of the endemic species in China and 16 long-tubed species and varieties (Wang & Li, 1999; Li et al., 2002). In the summers of 1993 and 1997, we made a preliminary study of the pollination biology of *Pedicularis* species in northwestern Yunnan (Wang & Li, 1998; Wang, 1998) and provided evidence in support of Macior's (1991) explanation of the function of the long-tubed species. Meanwhile, through insect bagging studies in Sichuan, Macior and Tang (1997, 1999) reported pollinator dependence of three *Pedicularis* species. However, knowledge of the pollination syndromes of *Pedicularis* in the Himalayas is far from adequate. Only the pollination syndromes of 2 (e.g., *P. siphonantha* D. Don var. *delavayi* (Franch. ex Maxim.) Tsoong and *P. longiflora* Rudolph var. *tubiformis* (Klotzsch) Tsoong) of the 16 long-tubed species in Yunnan have been documented. These, plus the other 2 species (*P. megalantha* D. Don and *P. punctata* Decne.) observed in the western Himalayas, were the only 4 long-tubed species studied by pollination biologists. This study aimed mainly to test the controversial explanations about the function of the long-tubed flowers and to compare it with the function of other types of corollas. One interesting question is whether the long-tubed species are pollinated by lepidopteran insects or by bumblebees and the evolutionary consequences. It is believed that more studies on the pollination biology in the species-richest area will provide more light on the cause of diversification of *Pedicularis*.

Table 1. Distribution of the four studied *Pedicularis* species.

Taxon	Distribution
Pedicularis densispica	Northwestern Yunnan, western Sichuan, southern and southeastern Xizang
P. integrifolia	Northwestern Yunnan, southwestern and western Sichuan, southeastern Xizang; Bhutan, Nepal, Sikkim
P. lutescens subsp. *lutescens*	Northwestern Yunnan
P. tricolor	Northwestern Yunnan

Materials and Methods

In the summer and fall of 2000, pollination investigations were conducted in alpine areas of the county of Zhongdian, northwestern Yunnan, China. We here report the pollination biology of four *Pedicularis* species in northwestern Yunnan, including two long-tubed species, *P. integrifolia* and *P. tricolor*, and two short-tubed, erostrate, and nectariferous species, *P. lutescens* subsp. *lutescens* and *P. densispica* (Tables 1–6).

Table 2. Flowering phenology of the four *Pedicularis* species at the study sites.

Taxon	Study site	Altitude (m)	First flowers–last flowers (2000)
P. lutescens subsp. *lutescens*	Tianshengqiao	3150	13 July–28 July
P. densispica			9 July–28 July
P. tricolor			19 July–15 August
P. integrifolia			27 June–21 July
P. integrifolia	Wufeng Mountain	3500	24 June–25 July
P. densispica	Jiantang	3300	7 July–26 July
P. tricolor		3150	15 July–9 August

Three sites were chosen for field observation, i.e., Tianshengqiao, Wufeng Mountain, and Jiantang. The first site, Tianshengqiao, featured dense populations of *Pedicularis*, with all four species in this study found in the open meadow. One population of *P. integrifolia* was relatively isolated on the north-facing slope of the second site in the Wufeng Mountains. *Pedicularis densispica* and *P. tricolor* were found in the third site at Jiantang.

Techniques in this study follow those of Macior (1968, 1977, 1988; Macior & Sood, 1990). Observations of bumblebee behaviors in the different populations of *Pedicularis* species were made at three sites of approximately 15 × 15 m, respectively. Records were made directly by close-range stereo-photography. Pollen analysis followed Erdtman (1969) and Wang et al. (2003) in designating pure, mixed, and foreign pollen.

All four *Pedicularis* species in the study sites were tested by bagging experiments to test dependence of these species upon insect pollinators. Ninety-eight pre-anthesal inflorescences of unopened buds for the four *Pedicularis* species were covered with galvanized window screen enclosures; another 68 flower inflorescences were not bagged as a control for open pollination. Fifty fresh flowers of each species were randomly selected to measure corolla tube length for each population of all four species at the three study sites. These flowers were examined by using light microscopes (60×) to check for the possibility of any existent nectar. The pollen/ovule ratio (p/o) was calculated after counting under a stereoscope as detailed by Cruden (1977) (see Table 6). Seed set was estimated in the late fall by opening fruit set of the 98 bagged and 68 control inflorescences (Table 5). A record of the blooming phenology of each species of *Pedicularis* in the three populations was maintained (Table 2). Voucher specimens of plants and insect pollinators from study sites were deposited at the herbarium of the Kunming Institute of Botany (KUN) (see Appendix 1).

Results

Plant Community Constituents and Floral Morphology, Phenology

The four *Pedicularis* species from the study sites are confined to the Himalayas (see Table 1). At the Tianshengqiao site, all four *Pedicularis* species were in bloom June–August 2000 in a rich, diverse, east-facing alpine meadow community (Table 2). *Pedicularis lutescens* subsp. *lutescens* was abundant there, while the other three *Pedicularis* species grew sparsely in open wet places. They were associated with *Drosera peltata* Smith subsp. *lunata* (Buch.-Ham. ex DC.) C. B. Clarke (Droseraceae), *Primula secundiflora* Franch. (Primulaceae), *Cynoglossum glochidiatum* Wall. ex Benth. (Boraginaceae), and *Ligularia lapathifolia* (Franch.) Hand.-Mazz. (Compositae). The meadow was close to a small hill dominated by *Quercus aquifolioides* Rehd. & Wils. (Fagaceae), *Populus szechuanica*

Table 3. Corolla tube length of the four studied *Pedicularis* species in northwestern Yunnan (based on 50 fresh flower measurements per population).

Pedicularis species	N	Mean length (mm)	Range (mm)
P. densispica	50	4.4	3.5–5.5
P. lutescens subsp. *lutescens*	50	8.0	7–10
P. integrifolia	50	32.7	31.0–35.0
P. tricolor	50	58.0	56.5–58.5

Table 4. Number of bumblebees observed on different species.

Taxon	Sites	*Bombus friseanus*	*Bombus lucorum*	*Bombus festivus*	Subtotal
Scrophulariaceae					
Pedicularis lutescens subsp. *lutescens*	Tianshengqiao	34 (81.0%)	8 (19.0%)		42
P. densispica		17 (94.4%)	1 (5.6%)		18
P. integrifolia		3 (100%)			3
P. tricolor		6 (100%)			6
Boraginaceae					
Cynoglossum glochidiatum		29			29 (29.6%)
P. integrifolia	Wufeng Mountain	5 (10.9%)		41 (89.1%)	46
P. densispica	Jiantang	287 (96%)	12 (4%)		299
P. tricolor		44 (96%)	2 (4%)		46
Fabaceae					
Medicago edgeworthii		218 (96%)	9 (4%)		227
Subtotal of all populations of four *Pedicularis* species		396 (86.1%)	23 (5%)	41 (8.9%)	460
Total		643	32	41	716

Schneid. (Salicaceae), and *Rhododendron axillaries* Franch. (Ericaceae).

Pedicularis integrifolia was the only *Pedicularis* species present at the Wufeng Mountain site. The dominant species associated with *P. integrifolia* here were *Caragana franchetiana* Kom. (Papilionaceae), *Pinus densata* Mast. (Pinaceae), and *Gymnadenia souliei* Schltr. (Orchidaceae).

At the Jiantang site, *Pedicularis densispica* and *P. tricolor* grew together in a dry sandy location with some *P. tricolor* along a dry sandy path. That site was close to farmland with cultivated *Brassica campestris* L. var. *oleifera* DC. (Brassicaceae), *Avena sativa* L. (Poaceae), and *Raphanus sativus* L. (Brassicaceae). Nearby, *Medicago edgeworthii* Sirj. (Fabaceae) and *Anaphalis contorta* (D. Don) Hook. f. (Compositae) were also in bloom in the summer of 2000.

In the three study sites, the four species of *Pedicularis* were in bloom from late June through early August 2000 (Table 2). *Pedicularis integrifolia* was the earliest-flowering of the four species in June. *Pedicularis tricolor* also opened 4 days earlier at Jiantang than at Tianshengqiao. In the Wufeng Mountains, flowering of the isolated population of *P. integrifolia* was also three days earlier than at Tianshengqiao in June.

The flower color is pale yellow in *Pedicularis tricolor* and in *P. lutescens* subsp. *lutescens*, while corollas are pale pink in *P. densispica* and purple in *P. integrifolia*. *Pedicularis lutescens* subsp. *lutescens* and *P. densispica* fall into the short-tubed, erostrate corolla type while *P. integrifolia* and *P. tricolor* are of the long-tubed, rostrate type, the upper corolla lip being extended into an S-shaped beak in *P. integrifolia* and a circular crest in *P. tricolor*. The

Table 5. Pollination-related fertility of the four *Pedicularis* species in study sites.

Taxon	Site	Bagged			Open-pollinated		
		Inflorescence	Flower	Fruits	Inflorescence	Flower	Fruits
P. lutescens subsp. *lutescens*	Tianshengqiao	25	201	6*	6	53	39
P. densispica		18	138	0	15	165	86
P. integrifolia		12	63	0	13	75	57
P. tricolor		9	80	0	2	13	8
P. integrifolia	Wufeng Mountain	7	39	0	7	43	32
P. densispica	Jiantung	9	113	5*	8	79	64
P. tricolor		18	252	3*	17	139	70
Total		98	886	14*	68	567	356

* Following destruction of floral enclosures by yaks.

Table 6. Ovule and pollen numbers and seed set.*

Pedicularis species	Capsule no.	Pollen grain/ flower (P)	Ovule number/ flower (O)	Pollen-ovule ratio	Seed set open pollination	Seed set bagged
P. lutescens subsp. *lutescens*	8	86,000 ± 38	116.7 ± 174.9	1484.9 ± 325.6	59.75 ± 13.15	0
P. densispica	15	182,850 ± 52	32 ± 2	5755.9 ± 906.8	9.6 ± 3.8	0
P. integrifolia	9	501,400 ± 138	64.5 ± 2.6	7765.3 ± 338.0	40.6 ± 41.4	0
P. tricolor	15	54,800 ± 55	31.75 ± 1.71	1908.1 ± 323.6	7.8 ± 4.4	0

* Values are means ± s.d.

lobes of the lower lip in *P. tricolor* are expanded into a broad bowl-shaped form subtending the beak (Fig. 1). The length of the corolla tube ranges from 32.7 mm in *P. integrifolia* to 58 mm long in *P. tricolor* to only 4.4 mm in *P. densispica* to 8 mm in *P. lutescens* subsp. *lutescens* (Table 3).

POLLINATOR BEHAVIOR AND FREQUENCY

The collection of 205 foraging bumblebees on the four species of *Pedicularis*, *Cynoglossum glochidiatum* Wall. ex Benth. (Boraginaceae), and *Medicago edgeworthii* (Fabaceae) was carried out with 86 man-hours in the three study sites. The insect specimens were used for taxonomic identification, frequency assessment, tongue length measurement, and analysis of corbicular pollen. A total of 205 corbicular pollen loads from foragers on the four species of *Pedicularis* was examined microscopically. Three bumblebee species, *Bombus friseanus*, *B. lucorum*, and *B. festivus*, were observed to forage on and pollinate the four observed *Pedicularis* species as well as other adjacent plants (Table 4).

All pollinators recorded on the four *Pedicularis* species were workers of three *Bombus* species, principally *B. friseanus* (86.1%; cf. Table 4), while queens were not observed. The short-tubed, erostrate flowers of *P. lutescens* subsp. *lutescens* and *P. densispica* were regularly visited by *Bombus friseanus* and *B. lucorum* workers for nectar and pollen in two sites. These workers scraped pollen from four anthers concealed within the galea (corolla upper lips) in an erect position. Pollen was dropped and deposited on the dorsal side of the bee's head and thorax. In *P. densispica*, *B. friseanus* workers approached the galea with antennae extended toward it (Fig. 2A) and grasped the lower lip with the forelegs (Fig. 2B). While foraging for nectar, the workers scraped and deposited pollen on the dorsal side of the thorax (Fig. 2C). A similar situation was observed in *P. lutescens* subsp. *lutescens*: the stigma protruding from the galea tip contacted pollen deposited on the bee's dorsal thorax (Fig. 2D, E). Both long-tubed and rostrate species (*P. integrifolia* and *P. tricolor*) were pollinated sternotribically by bumblebee workers; the bees grasped the flower while hanging in an inverted position with the ventral side of the thorax aligned with the opening in the galea through which pollen was released (cf. Macior, 1991). On Wufeng Mountain, workers of *B. friseanus* were also found foraging pollen on *P. integrifolia*, as at the Tianshengqiao site, but *B. festivus* workers were the principal pollinators at Wufeng Mountain (constituting 41 of 46 *Bombus* recorded, cf. Table 4). The workers of *B. festivus* grasped the long, S-shaped beak of *P. integrifolia* with all six legs (Fig. 2F), scraped pollen onto their ventral thorax and abdomen by hanging from the beak and vibrating the flower (Fig. 2G) with a buzzing sound while the stigma contacted residual pollen that was not transferred to the insects' corbicula. *Pedicularis tricolor* was mostly pollinated by *B. friseanus* workers (44 of 46 observations, or 96%). Pollinators grasped the lower part of the corolla beak first with forelegs, gradually with all six legs, hanging inverted from the corolla while being supported by the extended lower lip and scraping pollen, while the ventral thorax and abdomen directly contacted the stigma protruding from the tip of the galea (Fig. 2H).

Bumblebees began to visit and forage on *Pedicularis* species and adjacent plants at about 0800 hours, through 1700–1800 (Fig. 3). Peak visitation was between 1200 and 1500. *Bombus friseanus* appeared at about 0800 with an activity peak around 1400, while peak vistation activity for *B. festivus* was at 1600. *Bombus lucorum* appeared later at about 0900, with a peak at 1500 (cf. Fig. 3).

At each site the frequency of bumblebee species on the four studied *Pedicularis* species differed. Across all *Pedicularis* populations, *Bombus friseanus* formed 86.1% of the total followed by *B. festivus* (8.9%) and *B. lucorum* (5%). At Tianshengqiao, *Bombus friseanus* was the most abundant species on *P. lutescens* subsp. *lutescens* (34 of 42, or 81%) and *P. densispica* (17 of 18, or 94.4%) foraging for

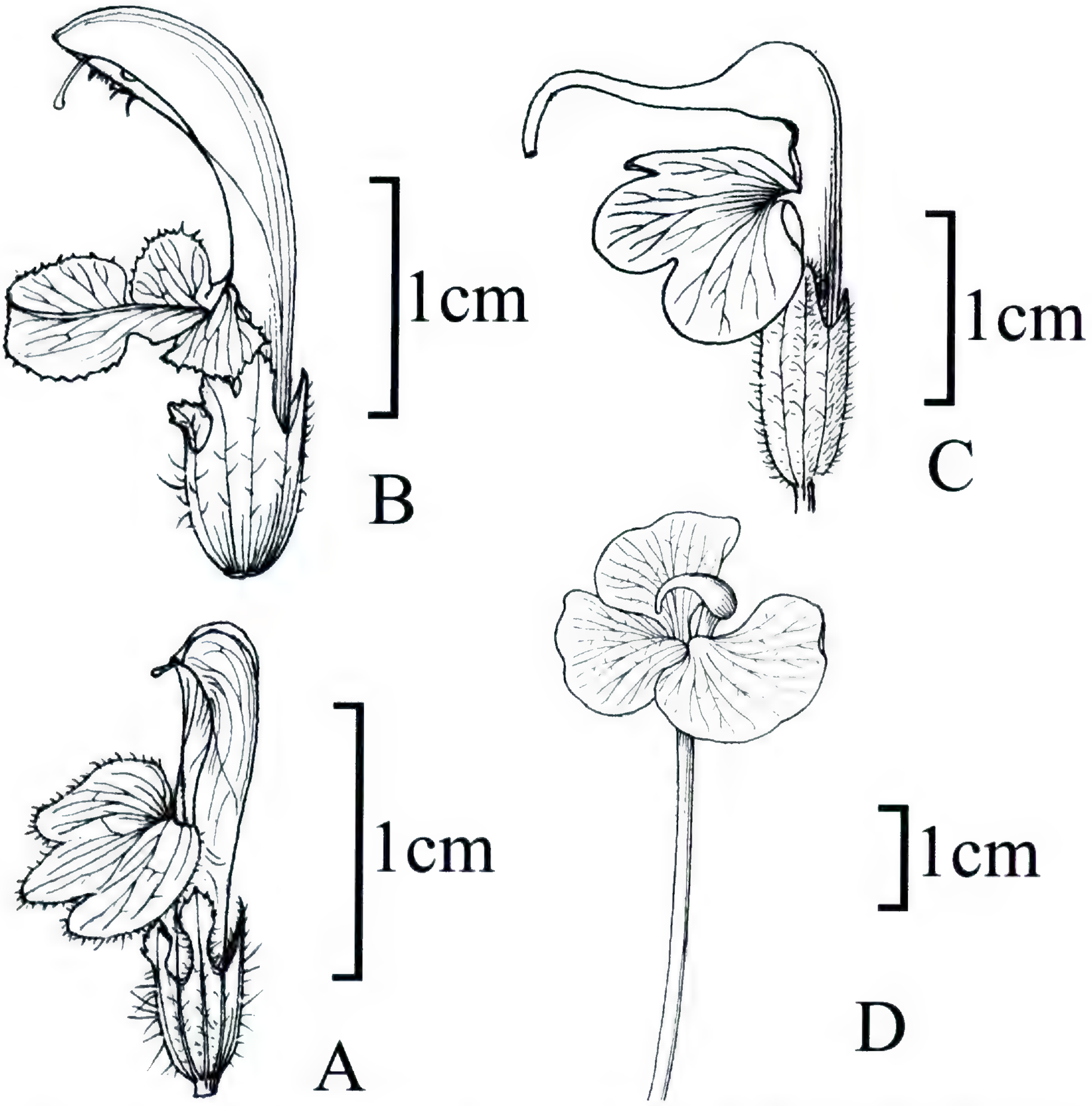

Figure 1. Corolla types of the four studied *Pedicularis* species. —A. *P. densispica*, corolla short-tubed, erostrate, and toothless. —B. *P. lutescens* subsp. *lutescens*, corolla short-tubed, erostrate, and toothed (with 4–10 teeth near the apex of each side of the galea). —C. *P. integrifolia*, corolla long-tubed, S-shaped beak. —D. *P. tricolor*, corolla long-tubed, upper corolla with a circular crest.

nectar and pollen (Table 4). Foragers alternately foraged on other flowers growing in the same site, notably *Cynoglossum glochidiatum*. A similar situation happened at Jiantang where the pollinators of *B. friseanus* (287 of 299, or 96%) appeared more frequently than *B. lucorum* (12 of 299, or 4%) on *P. densispica* and *Medicago edgeworthii* (also 96%) for nectar and pollen. For the two nectariferous *Pedicularis* species, *P. densispica* and *P. lutescens* subsp. *lutescens*, our field observations indicated that one flower of an inflorescence could be visited 6 to 10 times by different individuals of the same *Bombus* species; on nectarless species, a single flower was visited only 3 to 5 times by different individuals of the same *Bombus* species.

Corbicular pollen load analysis indicated 51.5% of *Bombus friseanus* carried *Pedicularis* pollen mixed with pollen from other species. *Pedicularis integrifolia* pollen was found in all loads of *Bombus festivus*, and the proportion of *P. integrifolia* pollen averaged 69.6%. *Bombus lucorum* carried 28% *Pedicularis* pollen (pers. obs., unpublished). The tongue lengths of the three observed *Bombus* species range from short (6.5–8.0 mm) in *B. lucorum* to long (9.0–11.0 mm) in *B. festivus*. Between them fell *B. friseanus* (7.0–8.8 mm) (Wang & Li, 1998).

Figure 2. *Bombus* foraging on *Pedicularis* flowers. A–C. *Bombus friseanus* worker pollinating *P. densispica.*—A. Bumblebee approaching flowers with antennae extended. —B. Grasping the lower corolla lip with the forelegs. —C. Nototribically contacting stigma. D, E. *Bombus friseanus* contacting pollen deposited on the dorsal side of the thorax on *P. lutescens* subsp. *lutescens.* F, G. *Bombus festivus* worker on *P. integrifolia.*—F. Grasping the S-shaped corolla beak with all six legs scraping pollen. —G. Hanging on the corolla beak and vibrating the flower. —H. *Bombus friseanus* worker supported by extended lower lip as a platform and scraping pollen on *P. tricolor.*

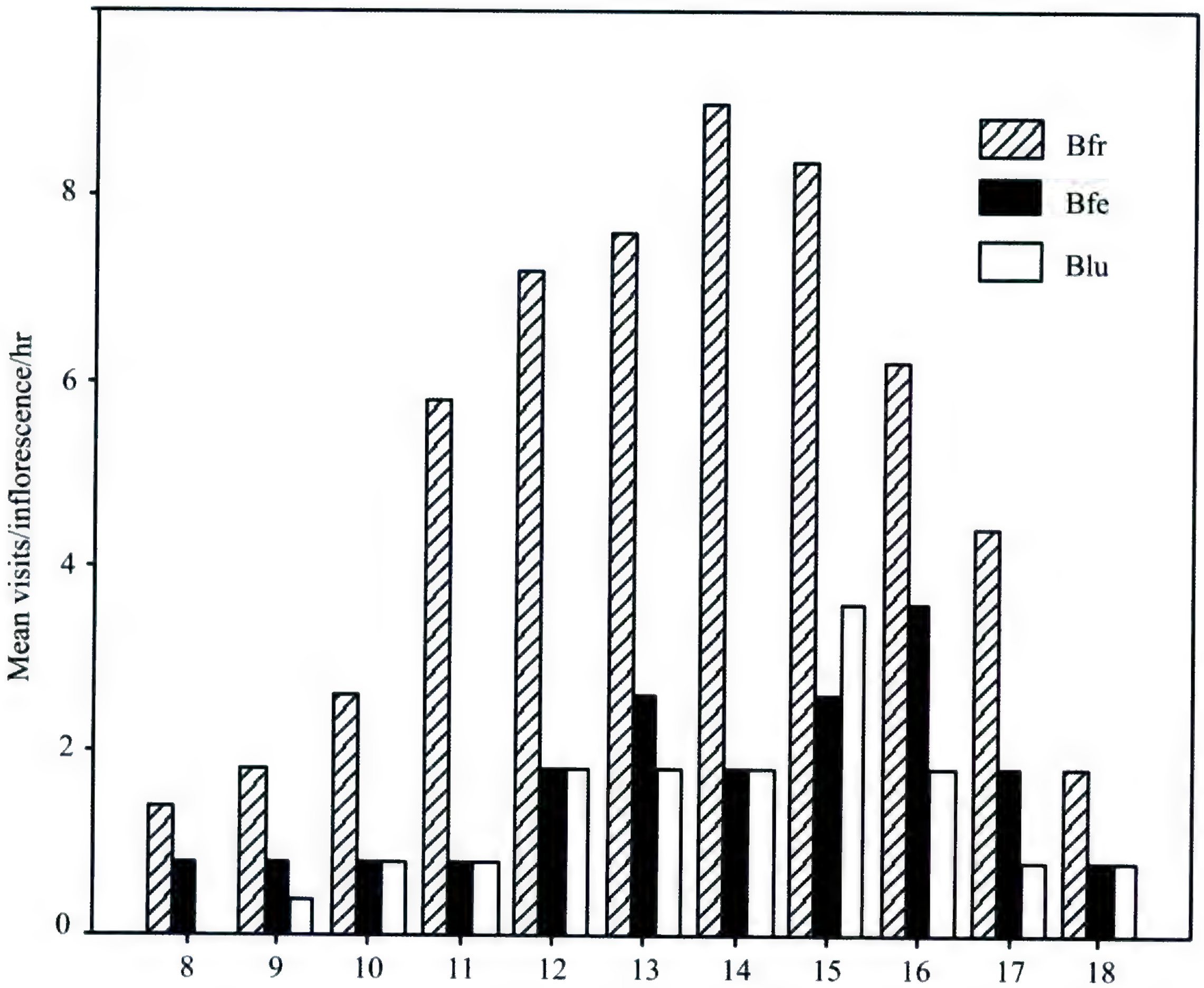

Figure 3. The visitation pattern of pollinators. Bfr = *Bombus friseanus*; Bfe = *B. festivus*; and Blu = *B. lucorum*.

It was noticed that three *Bombus* species with different tongue lengths might visit both *P. tricolor* (with a 58 mm long tube) and *P. densispica* (with a 4.4 mm long tube), as well as other flowering plants in the same population. Tongue length of *Bombus* pollinators and length of the corolla may not be correlated, as had been previously reported (Wang & Li, 1998).

FLORAL BIOLOGY AND MATING SYSTEM

Our study demonstrated that the four investigated *Pedicularis* species were incapable of unassisted self-fertility and were dependent on *Bombus* pollination for the production of seed. The only bagged inflorescences that produced fruits resulted from yaks destroying the plant enclosures (Table 5).

Pollen-ovule ratios may be used as a predictor of a plant's breeding system rather than floral size and morphology (Cruden & Miller-Ward, 1981). The highest p/o ratio was found in *P. integrifolia* with purplish pink flowers, while the lowest was *P. lutescens* subsp. *lutescens* bearing yellow corollas (Table 6). Similarly, the other yellow-flowered species, *P. tricolor*, also had a lower p/o ratio. Fruits were not developed in the bagged group, which suggested that the production of fruits in all four *Pedicularis* species was dependent upon pollen vectors in natural populations. In the open pollination group, the seed set of *P. lutescens* subsp. *lutescens* was the highest of the four species.

Discussion

POLLINATION MECHANISMS OF THE HIMALAYAN *PEDICULARIS* SPECIES, ESPECIALLY THE LONG-TUBED ONES

Pennell (1943) noted the exceeding diversity of corolla forms in *Pedicularis*. By attributing the differences in corolla form to the processes of pollination, he pointed out that this was a genus in

which field observations and the collecting of pollinators would be especially worthwhile. Earlier pollination studies on *Pedicularis* by Macior (1982, 1984, 1986) in North America, Japan (Macior, 1988), and the Kashmir Himalayas (Macior & Sood, 1990) revealed a general pattern of pollination in the genus, primarily associated with bumblebees. Pollination of the fourth floral form, i.e., the corolla with a beak and slender elongated tube, which occurs only in the Himalayas, was first reported by Macior & Sood (1990). He found that the magenta, nectarless, rostrate, long-tubed (to 2 cm) flower of *Pedicularis punctata* Decne. in the Kashmir Himalayas was pollinated by pollen-vibrating bumblebee workers. Our preliminary pollination observations on *Pedicularis* in northwestern Yunnan (Wang & Li, 1998) in the late summer of 1993 revealed that the yellow, nectarless, rostrate, exceptionally long-tubed (to 6 cm) flower of *Pedicularis longiflora* var. *tubiformis* was also pollinated by pollen-vibrating bumblebee workers. The present study demonstrates that the yellow, nectarless, rostrate, long-tubed (5.8 cm) flowers of *P. tricolor* are pollinated exclusively by *Bombus friseanus* and *B. lucorum* workers. As in *P. punctata*, *P. megalantha* (Macior & Sood, 1990), *P. longiflora* var. *tubiformis*, and *P. siphonantha* var. *delavayi* (Wang & Li, 1998), the long, nectarless corolla tube of *P. tricolor* appears to function in extending the rostrate vibration pollination mechanism beyond the plant's foliage and is not an adaptation for nectar-foraging lepidopteran pollinators, as suggested by Pennell (1943, 1948).

The pollen-vibration mechanism of the *P. tricolor* flower generally resembles the rostrate, nectarless, long-tubed floral mechanism as reported by Macior and Sood (1990) and Wang and Li (1998), but also differs markedly from them. In *P. punctata*, *P. siphonantha* var. *delavayi*, and *P. longiflora* var. *tubiformis*, the lower corolla lip is composed of three broad reflexed lobes and the corolla has a color contrast between the distal and proximal petal areas (purple vs. white in *P. punctata* and *P. siphonantha* var. *delavayi*, yellow vs. purple in *P. longiflora* var. *tubiformis*). In *P. tricolor*, the lower lip is composed of three much broader ascending lobes in a bowl-shaped form, which provides the *Bombus* pollinators a unique platform for scraping pollen. In *P. integrifolia*, the S-shaped beak is extremely long and robust, and the insects hang and scrape pollen without any support from the lower lip. Again, both *P. tricolor* and *P. integrifolia* are nectarless and do not appear to be pollinated by lepidopteran insects.

COMPARISON WITH THE POLLINATION SYNDROMES OF THE NORTH AMERICAN SPECIES

As pointed out by Macior (1988), a major determinant of pollination behavior is the form of flowers in *Pedicularis*. The erostrate species are pollinated by pollen-foraging bumblebee queens that vibrate or scrape pollen concealed within the galea (see Table 7). One exception is *Pedicularis furbishiae* S. Watson in Maine, U.S.A., and New Brunswick, Canada (Macior, 1978), which was previously thought to be the only nectariferous, erostrate, and short-tubed *Pedicularis* species that blooms in middle to late summer and is pollinated exclusively by bumblebee workers. Both *P. lutescens* subsp. *lutescens* and *P. densispica* are short-tubed, erostrate, and nectariferous species and were exclusively visited by *Bombus friseanus* and *B. lucorum* workers foraging for nectar and pollinating nototribically: they approached the tip of the galea and grasped the flowers; their heads were forced into the throat of the corolla and scraped pollen from four anthers concealed within the galea in the upright position. This is not in accordance with other erostrate and nectariferous species of *Pedicularis* vernally blooming in North America, but reveals a remarkable parallel to *P. furbishiae*.

Generally speaking, the floral form, floral color, and pollination behaviors on flowers of Chinese species of *Pedicularis* are comparable to those of North America and Japan. According to Macior (1978, 1982), *Pedicularis* species flowering in mid to late summer are nectarless, with the exception of the nectar-bearing *P. furbishiae*. Our study displayed a similar general pattern with the unique exceptions of *P. lutescens* subsp. *lutescens* and *P. densispica*.

Similar to the bagged experiments in *P. pulchella* Pennell of southwestern Montana and northwestern Wyoming, U.S.A. (Macior, 1986), as well as *P. palustris* L. and *P. sylvatica* L. in the northern Netherlands (Kwak, 1979), our bagged experiments and preliminary pollination controls showed that the production of seed in the four studied species of *Pedicularis* in northwestern Yunnan was dependent upon insect pollination, given the remarkably high difference in seed set between caged and open-pollinated flowers. Pollen/ovule ratio indicate that they are all incapable of unassisted self-fertility. Therefore, cross-pollination by bumblebee workers represents an important step in the reproductive biology of *Pedicularis*. Further work is needed with artificial cross- and self-pollination trials to examine their self-incompatibility.

As the bumblebee workers have a preference for

Table 7. Comparison of floral syndromes in *Pedicularis* in Yunnan, Himalayas, Japan, and North America.

Floral syndrome category in *Pedicularis*	Yunnan and Himalayan species	Japanese species	North American species*
1. Erostrate, nectariferous & nototribic	*P. lutescens* subsp. *lutescens* *P. densispica* aestival, by workers)	*P. apodochila* Maxim. **P. oederi* Vahl **P. verticillata* L.	*P. canadensis* L. *P. verticillata* (vernal, by *Bombus* queens) *P. capitata* Adams (early aestival, by queens and workers) *P. furbishiae* (aestival, by workers) *P. bracteosa* Benth. ex Hook.
2. Erostrate, nectarless & nototribic or polleniferous/sternotribic	**P. rex* C. B. Clarke ex Maxim. **P. roylei* Maxim. **P. tsekousensis* Bonati	Lack of data	
3. Erostrate, nectarless & sternotribic, by pollen-scraping	Lack of data	*P. chamissonis* Steven *P. resupinata* L. *P. yezoensis* Maxim.	*P. lanceolata* Michx.
4. Erostrate, nectarless & sternotribic, by vibration	Lack of data	Lack of data	*P. racemosa* Dougl. ex Hook.
5. Nectarless, short-tubed & nototribic, by vibration	Lack of data	Lack of data	*P. groenlandica* Retz.
6. Rostrate, nectarless, long-tubed & sternotribic, by vibration	**P. megalantha* **P. punctata* **P. siphonantha* var. *delavayi* **P. longiflora* var. *tubiformis* *P. integrifolia* *P. tricolor*	No such species available	No such species available

* Only examples are listed in this table (sources: Macior, 1988, 1991; Macior & Sood, 1990; Wang & Li, 1998; Wang, 1998).

foraging on the nectariferous flowers, as Macior (1978) suggested, nectar is a greater attractant than pollen. In California (Macior, 1977) and in the Himachal Himalayas, this competitive disadvantage for *Pedicularis* species was observed. In northwestern Yunnan, *Pedicularis* species were flowering with other sympatric, synchronous blooming, bumblebee-pollinated species, such as *Cynoglossum glochidiatum* and *Medicago edgeworthii*. However, the ecological or competitive consequences of such a situation need further investigation. The discovery of bumblebee workers as the exclusive pollinators of *P. tricolor* is in agreement with Macior (1991), who assumed that the mid-season flowering species represent a time when pollen foraging was emphasized by bumblebee brood-rearing with queens remaining in the nest.

DIVERSIFICATION OF POLLINATION MECHANISMS IN *PEDICULARIS* SPECIES

Maximowicz (1888) proposed the recognition of *Pedicularis* on the basis of four basic corolla types: (1) beakless, toothed, and short-tubed; (2) beakless, toothless, and short-tubed; (3) beaked, toothless, and short-tubed; and (4) beaked, toothless, and long-tubed. Li (1948, 1949, 1951) was the first to emphasize the importance of pollinator selection as a force in determining the diversification of floral forms in the genus. He emphasized that parallel evolution had occurred in corolla morphology by clearly defining the series according to the four corolla types proposed by Maximowicz. He assumed that in *Pedicularis* toothed corollas were derived from toothless, beaked from non-beaked, and long-tubed from short-tubed, under the pressure of pollination and adaptation to pollinator insects. Tsoong (1955, 1956) proposed another important classification for the genus, which was similar to Li (1948, 1949, 1951) in that all the species in each primary group had the same phyllotaxy. However, Tsoong did not place as much importance on phyllotaxy as Li did.

Based on pollination function and phenology of bloom, the floral syndromes of *Pedicularis* were

classified into six categories (Macior, 1991) (Table 7). No data were available for two major types, i.e., the erostate, nectarless, and sternotribic type and the nectarless, short-tubed type, of *Pedicularis* in Yunnan. Study of these pollination syndromes is needed for an understanding of the evolution of floral forms in *Pedicularis* in relation to their adaptation to pollination pressure, especially in this center of diversification for *Pedicularis* in the Himalayas (Hong, 1983).

As for the four recognized corolla types in the genus, the fourth type, the nectarless, rostrate, and long-tubed one is restricted to Yunnan, Sichuan, and the Himalayas. The presently available information for studied species in the Chinese Himalayas (Macior & Tang, 1997, 1999; Wang & Li, 1998; Macior et al., 2001) reveals a similar pattern of pollination syrdrome description as in North American species. Further study in the early spring, and on the rostrate and short-tubed, nectarless species in Yunnan will fill in our gaps of knowledge of pollination syndromes in the entire genus. By studying the pollination ecology of Japanese *Pedicularis*, Macior (1988) proposed that the Japanese species evolved in a pattern parallel to that pursued by North American species from Himalayan migrants. In general, our present and previous studies provide evidence in support of this hypothesis. Further evidence is needed to understand the evolution of this important and interesting genus, e.g., pollen morphology and its relationships with pollination syndrome (Wang et al., 2003), chromosome numbers and karyotype morphology (Cai et al., 2004), and, in particular, molecular phylogeny (Ree, 2001).

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Appendix 1. A list of voucher specimens for pollination studies. All voucher specimens were collected in Zhongdian county, northwestern Yunnan, China, and were deposited in KUN.

Scrophulariaceae

Pedicularis densispica Franch. ex Maxim.: *Hong Wang 0021*, Tianshengqiao; *Hong Wang 0065*, Jiantang.

P. integrifolia Hook. f.: *Hong Wang 0022*, Tianshengqiao; *Hong Wang 0034*, Wufeng Mountains.

Pedicularis lutescens Franch. ex Maxim. subsp. *lutescens*: *Hong Wang 0023*, Tianshengqiao.

P. tricolor Hand.-Mazz.: *Hong Wang 0024*, Tianshengqiao; *Hong Wang 0066*, Jiantang.

Boraginaceae

Cynoglossum glochidiatum Wall. ex Benth.: *Hong Wang 0028*, Tianshengqiao.

Fabaceae

Medicago edgeworthii Sirj.: *Hong Wang 0071*, Jiantang.

Apidae (Insecta)

Bombus festivus Smith: *Hong Wang 115*, Wufeng Mountains.

Bombus friseanus Skorikov: *Hong Wang 63*, Tianshengqiao; *Hong Wang 127*, Wufeng Mountains; *Hong Wang 150*, Jiantang.

Bombus lucorum Latr.: *Hong Wang 68*, Tianshengqiao; *Hong Wang 147*, Jiantang.

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CONTENTS

Conservation Genetics, the 19th Annual Systematics Symposium of the Missouri Botanical Garden

Conservation Genetics: Theory and Practice — *Barbara A. Schaal & Wesley J. Leverich* 1

Theory and Methods for Diagnosing Species and Populations in Conservation — *Paul Goldstein, Yael Wyner, Phaedra Doukakis, Mary G. Egan, George Amato, Howard Rosenbaum & Rob DeSalle* 12

Adaptive Radiation and Regulatory Gene Evolution in the Hawaiian Silversword Alliance (Asteraceae) — *Michael D. Purugganan & Robert H. Robichaux* 28

Using *Mimulus* as a Model System to Understand the Role of Inbreeding in Conservation: Genetic and Ecological Approaches — *Michele R. Dudash, Courtney J. Murren & David E. Carr* 36

Loss of Genetic Diversity and Erroneous Phylogeographical Inferences in *Lithocarpus konishii* (Fagaceae) of Taiwan Caused by the Chi-Chi Earthquake: Implications for Conservation — *Kuo-Hsiang Hung, Tsai-Wen Hsu, Barbara A. Schaal & Tzen-Yuh Chiang* 52

Phylogenetics of Amaranthaceae Based on *mat*K/*trn*K Sequence Data—Evidence from Parsimony, Likelihood, and Bayesian Analyses — *Kai Müller & Thomas Borsch* 66

Resurrection and Revision of *Patima* (Rubiaceae, Cinchonoideae, Hamelieae) — *Piero G. Delprete, Michael Nee & Jifke Koek-Noorman* 103

A Review of Hybridization in North American Hawthorns—Another Look at "The *Crataegus* Problem" — *J. B. Phipps* 113

Pollination Biology of Four *Pedicularis* Species (Scrophulariaceae) in Northwestern Yunnan, China — *Hong Wang & De-Zhu Li* 127

Cover illustration. *Megacorax gracielanus* S. González & W. L. Wagner, first described as a new genus and species of the family Onagraceae from Mexico in *Novon* 12: 362. 2002. The generic name is based on the combination of the Greek words *mega*, large or great, and *korax*, raven, to honor Missouri Botanical Garden Director Peter H. Raven, author of numerous papers and monographs on many aspects of the family and one of our foremost advocates for conservation and sustainable use of the environment. The specific epithet honors Graciela Calderón Díaz-Barriga, major contributor to *Flora del Valle de México* and *Flora del Bajío* and mentor of several generations of students. The illustration is by Alice R. Tangerini (US).

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AFRICAN PLANT DIVERSITY AND CLIMATE CHANGE

Colin J. McClean,[2] *Jon C. Lovett,*[2,6] *Wolfgang Küper,*[3] *Lee Hannah,*[4] *Jan Henning Sommer,*[3] *Wilhelm Barthlott,*[3] *Mette Termansen,*[2] *Gideon F. Smith,*[5] *Simon Tokumine,*[2] *and James R. D. Taplin*[2]

ABSTRACT

International goals have been set to protect global plant diversity and limit ecosystem damage due to climate change, but large-scale effects of changing climate on species distributions have yet to be fully considered in conservation efforts. For sub-Saharan Africa we study the shifts in climatically suitable areas for 5197 African plant species under future climate models for the years 2025, 2055, and 2085 generated by the Hadley Center's third generation coupled ocean-atmosphere General Circulation Model. We use three species distribution models, a "Box model," a simple genetic algorithm, and a Bayes-based genetic algorithm. The results show major shifts in areas suitable for most species with large geographical changes in species composition. The areas of suitable climate for 81%–97% of the 5197 African plant species are projected to decrease in size and/or shift in location, many to higher altitudes, and 25%–42% are projected to lose all of their area by 2085. In particular, the models indicate dramatic change in the Guineo-Congolian forests, mirroring proposed ecological dynamics in the past. Although these models are preliminary and may overestimate potential extinctions, they suggest that efforts to protect African plant diversity should take future climate-forced distribution changes into account.

Key words: Africa, biodiversity, climate change, conservation, extinction, Global Strategy for Plant Conservation (GSPC), Important Plant Areas.

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[2] Centre for Ecology, Law and Policy, Environment Department, University of York, Heslington, York YO10 5DD, United Kingdom.

[3] Nees Institute for Biodiversity of Plants, University of Bonn, Meckenheimer Allee 170, D-53115 Bonn, Germany.

[4] Center for Applied Biodiversity Science, Conservation International, 1919 M Street NW, Washington, DC 20036, U.S.A.

[5] South African National Biodiversity Institute, Private Bag X101, Pretoria, South Africa, and Department of Botany, Herbarium, University of Pretoria, 0002, Pretoria, South Africa.

[6] Corresponding author.

Biodiversity conservation is typically implemented by delimiting a piece of land as a site of special scientific interest, nature reserve, or national park. This has the advantage of permitting a set of management criteria to be applied to a clearly defined area with discrete boundaries and can be used to preserve both particular types of ecosystems and rare organisms. Alternatively, certain species can be protected by creating a list of key taxa, such as Red Lists (Baillie et al., 2004) or species appended to the Convention on International Trade in Endangered Species (Ong, 1998), that have a legal status that prevents them from being interfered with even though they might occur outside areas designated for nature conservation. This is useful for uncommon taxa with a wide range, migratory species, and plants and animals of special significance. However, climate change may result in significant distributional shifts of entire ecosystems, and the creation of novel community associations as species respond to new conditions in an individualistic manner. This might make existing networks of protected areas redundant and lists of legally protected taxa inadequate. The prospect of increased climate dynamics has led to a proposal for "climate change-integrated conservation strategies," the first step of which is to undertake regional modeling of biodiversity response to climate change (Hannah et al., 2002b: 265).

Plant conservation has recently been given a major boost with the creation of the Global Strategy for Plant Conservation (GSPC) by the sixth meeting of the conference of the parties to the Convention on Biological Diversity (CBD) held in The Hague in April 2002 (Convention on Biological Diversity, 2002). Arising from the keynote address by Peter Raven to the 1999 International Botanical Congress in St. Louis, Missouri, which called for efforts to save the 300,000 kinds of plants in the world (Raven, 2004: 103), the primary objective of the GSPC is "*to halt the current and continuing loss of plant diversity*" (Convention on Biological Diversity, 2002: 3), which it aims to do by meeting 16 targets by the year 2010. Target five is "*Protection of 50 per cent of the most important areas for plant diversity assured*" (Convention on Biological Diversity, 2002: 7), giving rise to the concept of Important Plant Areas as a conservation tool (Anderson, 2002; Plantlife, 2004). The first steps to establishing the criteria needed to draw up a list of Important Plant Areas for Africa were taken at meeting of the Southern African Botanical Diversity Network (SABONET) in Pretoria 10–14 May 2004 (Lovett, 2004; SABONET, 2004; Smith & Smith, 2004).

Here, we consider the effects of projected climate changes on continental-scale distribution of African plant species, changes that have important implications for nations attempting to meet the GSPC targets, especially since Africa is thought to be the continent most vulnerable to climate change (IPCC, 2001). We conclude that climate change over the next 50 to 80 years, under current greenhouse gas emissions scenarios, will have a major impact on the location and nature of African plant diversity and needs to be taken into account when defining Important Plant Areas.

Methods

Species Data

Since 2003 data on Africa-wide plant distributions have been contributed by various research institutions to a Biogeographic Information System on African Plant Diversity (BISAP), which is hosted and curated at the Nees Institute for Biodiversity of Plants (BIOMAPS project within the BIOLOG BIOTA framework). The data have been used for a variety of analyses of African plant diversity (Lovett et al., 2000; La Ferla et al., 2002; Taplin & Lovett, 2003; Burgess et al., in press; Küper et al., 2004; Linder et al., 2005). Examples of distribution patterns can be seen on the Centre for Ecology, Law and Policy (2004) plant mapping website <http://www.york.ac.uk/res/celp/webpages/projects/worldmap/worldmap.htm>.

The species database includes over 6200 taxonomically revised species with more than 330,000 distribution records from confirmed collection localities. Requests for information concerning the plant distribution database should be directed to Wolfgang Küper (e-mail address: wk@uni-bonn.de). For this study, only the 5197 species occurring on the African mainland south of latitude 27°N with distribution records in at least two grid cells have been considered: a total of 93,715 one-degree grid cell records. The sample accounts for between 10% and 15% of the African flora (Beentje et al., 1994) and 1.6% of the world's plant species (Barthlott et al., 1999; Prance et al., 2000). Plant distribution data from north of latitude 27°N are too sparse for the purposes of modeling. Spatial resolution of the plant distribution data used here varies between point data, mainly from herbarium collections with georeferenced localities, to 1° resolution data from digitized maps. All distribution data were rescaled to a one-degree latitude-longitude grid. Although these are the most comprehensive data ever assembled for the study area, many species may occur in more than the currently documented grid cells, a

Table 1. The climate variables used for all models.

Variable name	Variable description
MTW	Mean temperature of the warmest month
MTC	Mean temperature of the coldest month
ATR	Annual range of mean monthly temperature
MINTC	Mean minimum temperature of coldest month
MAXTC	Mean maximum temperature of warmest month
AMIN	Absolute minimum temperature
MAP	Mean annual precipitation
MAPD	Mean annual precipitation of the driest month
AMI	Annual moisture index

problem inherent in most biogeographic data sets (Williams et al., 1996).

CLIMATE DATA

Climate predictions are from the Hadley Centre's third generation coupled ocean-atmosphere General Circulation Model, HadCM3B1 (The Climate Impacts LINK Project, 2004 <http://www.cru.uea.ac.uk/link/new_link/welcome.html>). The B1 scenario has been developed by the IPCC (Nakićenović & Swart, 2000) and describes the most conservative estimate of climate change from the HadCM3 output. Climate scenarios were developed around the four time periods of 1975, 2025, 2055, and 2085 based on 30-year averages. Data representing an average around the year 1975 were used as present climate variables on which to base each species model. The GCM data are provided at a global scale in a non-regular 2.5 × 3.75 degree grid structure. In order to maintain consistency with the regular 1-degree resolution of the continental-scale plant species data, the GCM data were converted to lattices of points from which 1 × 1 degree continuous surfaces were interpolated (Carter et al., 1999) using a simple inverse distance weighting method using the eight nearest neighbors. The variables used in the continental scale modeling are given in Table 1. Absolute minimum temperature was calculated following Prentice et al. (1992). Annual moisture index is the quotient between mean annual precipitation and mean annual potential-evapotranspiration. The latter was calculated using the Thornthwaite equation (Stephenson, 1998) incorporating a latitude-based estimate of day length (Forsythe et al., 1995). The elevation data used in the study were the GTOPO30, 30 arc-second gridded digital elevation model for the globe (Land Processes Distributed Active Archive Archive Center, 2004 <http://edcdaac.usgs.gov/gtopo30/gtopo30.asp>).

MODELING

We used distribution modeling that matches the location of observed species occurrence records with the spatial partitioning of appropriate climate variables. These types of models have also been variously described as niche models and bioclimatic envelopes (MacArthur, 1972; Huntley et al., 1995; Pearson et al., 2002; Peterson et al., 2002; Pearson & Dawson, 2003). In order to evaluate the sensitivity of our biological conclusions to methodological details we used three distribution model variants derived from currently available methods. The first (BOX) is similar to a "Box model" (Box, 1981), which represents the full range (extremes) of climate space a species is observed to inhabit. The second method attempts to find the environmental range that maximizes the number of correctly predicted occurrences while minimizing overprediction of species presence using a simple genetic algorithm (SGA). The third method, a Bayes-based genetic algorithm (BGA), calculates the probability of occurrence for a species given a set of climatic variable thresholds using a Bayesian classifier and a genetic algorithm. We assume either full dispersal or no dispersal (Peterson et al., 2002; Thomas et al., 2004a). Full dispersal assumes that species can disperse from one location in Africa to any other location irrespective of distance; no dispersal assumes that species cannot disperse to other grid cells. Once we have modeled a species using current climate spatial distributions, we can observe where the climate would be expected to be suitable for the species under future climate predictions.

Ideally, from a modeling perspective, all species would have a large number of presence observations, as this would allow species data to be split into calibration and validation data sets that could be used to test the predictive accuracy of the models. However, Stockwell and Peterson (2002) demonstrated the problem associated with not including data: accuracy of models appears to increase as more observations are included. This would become a major issue when analyzing plants with a small number of observations. We have, therefore, used all available records for each species. Not doing so could result in us missing out observations that give important information about the current climate conditions in which the plant is found. The three modeling techniques are described in more detail

below. The three different algorithms were coded in "C" and input-data stored as ascii files in ESRI's Grid format. Spatial data handling prior to running the models, as well as the handling of spatial results, was performed using the GRASS 5.3 GIS software <http://grass.itc.it>). Cartographic output was produced using ArcView 3.3.

THE BOX MODEL

For the BOX model each species distribution record is overlain with each climate variable in turn. For each climate variable, the maximum and the minimum values found at the location of the distribution records are recorded. Nine climate surfaces are used in the analysis, and these define a nine-dimensional climate envelope. If the areas falling within each of the ranges given by the nine minimum and maximum values for the nine climate surfaces are mapped, this provides an indication of all the areas that might be climatically suitable for the species. All the species presence observations will be contained within this mapped envelope, but so too will many areas without a distribution record. The BOX model therefore tends to overpredict species occurrences. No weights are given to the various climate thresholds that might be most important to the species; in this way a future climate change in any one of the variables used to produce the model can result in areas that were previously climatically suitable being deemed as climatically unsuitable. Adaptations of this method have been used in a number of previous studies (Box et al., 1993, 1999; Crumpacker et al., 2001). To assess the fit of predicted to observed patterns of individual species models, we use the kappa coefficient, which attempts to balance the assessment of errors of both omission and commission resulting from the model (Manel et al., 2001). Based on the confusion matrix produced by comparing two classifications, in our case a simple cross-tabulation of observed presence/absence with predicted presence/absence, this coefficient can take a value from 0, complete disagreement between predicted and observed, to 1, complete agreement between predicted and observed. Kappa was calculated using observed and predicted presence/absence maps in GRASS 5.3.

GENETIC ALGORITHMS

The genetic algorithms (GA) seek to identify the distribution of climate variables that give the closest match to the observed species presence patterns. Both GA approaches used in this study share the basic approach behind all genetic algorithms; in the context of bioclimatic modeling these are as follows.

The genetic algorithm starts with a "population" of possible climate variable ranges, known as "chromosomes." These ranges are obtained by taking subsections of the full ranges that occur in the study area. One possible chromosome is the set of ranges used in the BOX model. Another example would be a chromosome from the population that has a minimum value for mean maximum temperature of the warmest month of 25°C, a maximum value for mean maximum temperature of the warmest month of 32°C, a minimum value for mean annual precipitation of 600 mm, a maximum value for mean annual precipitation of 850 mm, and so on, until ranges are defined for each of the climate variables included in the analysis. Each minimum or maximum value represents one "gene" on a chromosome. Genes are allocated randomly to the initial population from within the full climate variable ranges that occur in the study area. The areas accounted for by the set of variable thresholds contained in the genes of a chromosome can be mapped and compared to the observed distribution. A score can be calculated to measure how well that chromosome captures the observed plant distribution. Continuing the natural selection analogy, this score is described as the fitness of the chromosome.

On the basis of their fitness values, members of the population are allowed to reproduce. If a chromosome has a high fitness score, it has a higher probability of reproducing with another chromosome from the population. Reproduction occurs by taking a number of genes from one chromosome and a number of genes from the other chromosome. This is analogous to the biological phenomenon of crossover, in which two offspring chromosomes are produced. In this way genes that provide good solutions are taken from successful individuals into the next generation in a search for the optimal solution. However, the genes of the initial population may not be the genes that can provide the best possible fit between the climate variables and the observed species distribution. In an attempt to avoid local maxima resulting from the limited nature of the genes of the initial population, an operation known as mutation is added to the algorithm. A mutation operation simply allows the value of a randomly selected gene on a randomly selected chromosome to be changed by a random number. Mutations can survive into future generations if the fitness scores of the mutated chromosomes are high enough to allow them to reproduce. The algorithm advances through generations of solutions until no noticeable improvements are made to the fitness

score of the fittest chromosome. The difference between the Simple Genetic Algorithm (SGA) and Bayes-based Genetic Algorithm (BGA) models used here is the measure of fit used to assess how well the pattern predicted by a chromosome fits the observed species presence pattern, which is termed the fitness score.

SIMPLE GENETIC ALGORITHM (SGA) MODEL

The fitness score used in this method is Dice's or Sørensen's index (Krebs, 1999). This compares the number of correct predictions with the number of overpredictions as follows:

$$s = \frac{2a}{a + b + c}$$

where s is Sørensen's index; a is the number of correct predictions; b is the number of false positives; c is the actual number of presence observations. If the number of correct predictions equals the number of actual presence observations, the number of overpredictions is zero and the index will equal one.

The effect of using this index as the fitness score measure for chromosomes in the GA is that observed species presences are traded off against overpredictions. So observations on the edge of the BOX model can be left out of the solution allowing narrower thresholds within the climate ranges to be found. In this way the SGA approach can be more sensitive to the variables that constrain the model most. Once again, in future time periods if a location falls outside the thresholds found for any of the climate variables used to determine the model, the location will be deemed to have climate unsuitable for the species. As with the BOX models, the quality of SGA model results were also assessed using the kappa coefficient.

BAYES-BASED GENETIC ALGORITHM (BGA)

The fitness score used in this method involves Bayes's theorem and is based on predictive modeling approaches using Geographical Information Systems (GIS) (Aspinall, 1992; Tucker et al., 1997). Bayes's theorem in this application can be stated as follows:

$$P(Y \mid X_1 \cap X_2 \cap X_3 \cdots X_n) = \frac{P(Y)\prod_{i=1}^{n} P(X_i \mid Y)}{P(Y)\prod_{i=1}^{n} P(X_i \mid Y) + P(notY)\prod_{i=1}^{n} P(X_i \mid notY)}$$

where event Y is the presence of a species and $notY$ is the absence of a species, X_i is the presence of a climate variable, i, within certain minimum/maximum thresholds. The left-hand side of the equation is the probability of the event that a species is present given the occurrence of the set of n climate variable thresholds (known as the posterior probability). For each chromosome in the GA, the minimum, maximum gene couplets represent the X_i. Within a raster- or point-based GIS environment, the $P(X_i \mid Y)$ and $P(X_i \mid notY)$ terms can be calculated by counting the pixels/points between the minimum and maximum values provided by the genes that occur where the species is present (Y) or absent ($notY$). By using the formula for the combination of climate variable ranges, given by a chromosome, for each pixel/point we obtain a posterior probability of finding the species. These maps of posterior probability can then be analyzed to produce the final fitness score: the difference between the average probability for pixels/points with the species and the average probability for pixels/points without the species. In this case the GA's solution to maximizing the fitness score settles on the climate variable ranges that separate presence and absence pixels/points. By studying the magnitude of the difference between the $P(X_i|Y)$ and $P(X_i|notY)$ terms for the best chromosome obtained by the GA, we can interpret which factors have most influence on the final posterior probability scores and therefore which climate variables appear most important to the species. For the species studied here, the number of times each climate variable is found to be most important to the model definition is recorded in Table 2. The predictive ability of models based on presence/absence data, where estimates of the probability of occurrence for each observation are provided, can be assessed by constructing the relative operating characteristics curve (ROC). The area under this curve (AUC) pro-

Table 2. Frequency with which climate variables are found to be the most important model variables (BGA method).

Variable name	Frequency	Percentage	Cumulative percent
MAP	1022	19.7	19.7
MTW	822	15.8	35.5
AMI	760	14.6	50.1
MAXTC	562	10.8	60.9
ATR	507	9.8	70.7
MAPD	479	9.2	79.9
AMIN	374	7.2	87.1
MINTC	350	6.7	93.8
MTC	321	6.2	100

vides the assessment of the predictive abilities of the model (Pearce & Ferrier, 2000). This value can vary from 0.5, the model has no predictive ability, to 1, perfect ability to predict. We calculate the AUC score for each species model when using the BGA approach.

CALCULATING ELEVATION DATA FOR CLIMATE MODEL PREDICTIONS

From the original 30 arc second raster data, the median elevation of each one-degree grid cell in the African study area was calculated. For each individual species in the BOX and SGA model results, the average of the one-degree median elevation values was calculated for cells that were predicted to contain suitable climate. For the BGA model, probability of suitable climate occurrence was used to calculate a weighted mean elevation for each species model.

CALCULATING FLORISTIC TURNOVER FOR EACH GRID CELL

Dice's or Sørensen's index was used to assess the amount of change between present and future periods in each one-degree cell:

$$s = \frac{2a}{a + b + c}$$

where a is now the number/level of probability of species with suitable climate found in a cell for both the future period and the present; b is the number/level of probability of species with suitable climate entering a cell in the future, but not found in the present model; c is the number/level of probability of species with suitable climate found in the present period. If all species with suitable climate found in the present period are also found in the future period and there are no additional species, the index will have the value one.

CALCULATING AVERAGE CLIMATE VARIABLE VALUES FOR SPECIES PRESENT PREDICTIONS

It is difficult to obtain a measure of how particular changes in individual climate variables will affect plant diversity across Africa because of the multidimensional nature of the climate spaces we consider. We can, however, consider how these variables are predicted to change over the study periods in the geographical areas that currently have suitable climate for the species. To do this for the BOX and SGA models of each individual species, the average of each climate variable was calculated for cells that were predicted to contain suitable climate in the present period; for the same cells, these statistics were calculated for each of the future periods. For the BGA model the probability of suitable climate occurrence was used to calculate a weighted mean for each species' model. Examples of the distributions obtained for a temperature and a precipitation variable are given in Figures 1 and 2.

Results

For each modeling approach and for each one-degree grid cell, summing across model predictions for each species allows an assessment of the number of species bioclimatic envelopes that are suited to the environment of a cell. Comparison of these summations with the number of species actually observed in each grid cell (species richness) demonstrates that areas of suitable contemporary climate for varying numbers of species are well correlated with observed species richness for the SGA and BGA models (r_s = 0.75 and 0.73, respectively), while the BOX model is less well correlated (r_s = 0.52) because this climate distribution model includes the most extreme climate variable values found for each species. These overall patterns are in agreement with the assessments of individual model performance. The BOX models have a symmetrical distribution of kappa coefficients with a mean value of 0.548 and a standard deviation of 0.332. The SGA model results have a negatively skewed distribution of kappa coefficients with a median value of 0.716 and an interquartile range of 0.358. Three-quarters of the models have a value above 0.530. The distribution of BGA model AUC scores is negatively skewed with a short tail of poor AUC scores. The median AUC score is 0.971 with an interquartile range of only 0.098. Only 61 of the models give an AUC score of less than 0.75.

By 2085, models show that between 81% and 97% of species have lost areas of suitable climate across the study area (Table 3). Species losing some area of suitable climate greatly outnumber species gaining area of suitable climate (using the full dispersal assumption) in all scenarios and for all models. Loss in area of suitable climate for individual species is most pronounced under the BOX and SGA models, because these models deem a cell unsuitable if even one future climate variable value for the cell falls outside the modeled climate niche of the species. The BGA model allows the probability of occurrence of climatic suitability to be reduced as climate changes, rather than predicting complete unsuitability. As a result, it provides consistently lower estimates of change when these probabilities are summed across Africa.

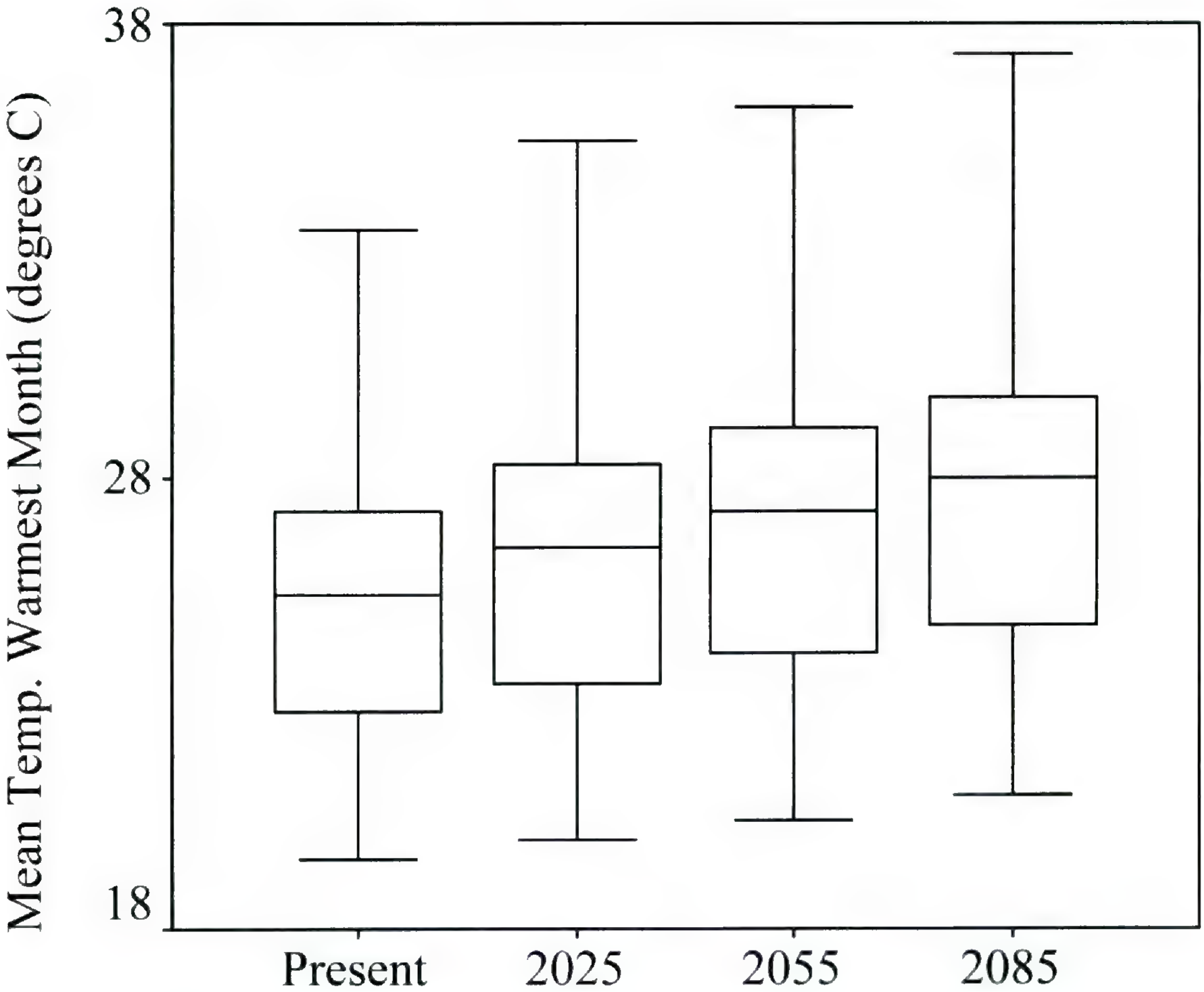

Figure 1. Box-plots of the mean temperature of the warmest month for grid cells detected as areas of suitable climate for each species under current predictions. Middle line in boxes gives median value for 5197 species. Upper line of box gives upper quartile, while lower line gives lower quartile. Whiskers extend over range after outliers and extremes have been removed. These results are for the BGA model.

Extinction risk may be estimated by the number of species that lose all suitable climate in a future scenario. Total loss of all area of suitable climate is projected for 25%–57% of species by 2085 under the full dispersal assumption and 34%–76% if no dispersal is assumed. Some 19% (full dispersal) to 28% (no dispersal) of our sample species are projected to lose all areas of climate suitability by 2055, in our conservative BGA model. The values are higher than estimates of 4%–19% of species projected to lose all of their suitable climate space by 2050 in a recent study (Thomas et al., 2004a, b), but for the most part lower than the 15%–37% (mid-range climate scenario) of species predicted to become extinct in the long run by the methods of the same study that extrapolate extinction risk for species with reduced areas. Adopting the latter methods would increase our estimates of extinction risk in all scenarios and models. Importantly, by 2085 even our most conservative model and dispersal assumptions project that 25% of species will lose all of their climatically suitable area, close to the predicted long-term extinction levels estimated by Thomas et al. (2004a) for climate change by 2050.

To estimate the geographic distribution of these changes under the assumption of full dispersal, we calculated the percentage change in the number of species for which a grid cell is predicted to be climatically suitable between present and future periods (Fig. 3a–i). This gives a view of the dynamics of changing areas of climate suitability across time. The three models agree on a number of trends. Many species lose climatically suitable areas from "hotspots," which are already recognized as centers of high biodiversity under severe threat (Myers et al., 2000; Küper et al., 2004). All models show progressive loss of areas of suitable climate for species in the Guineo-Congolian rain forests of West and Central Africa, including the central Congo Basin, accompanied by gains in surrounding uplands. Other highland areas such as the Drakensberg Mountains and Namibian Highlands also potentially provide areas of suitable climate for many species new to these regions. In eastern Africa, the Eastern Arc and Coastal Forests of Tanzania and

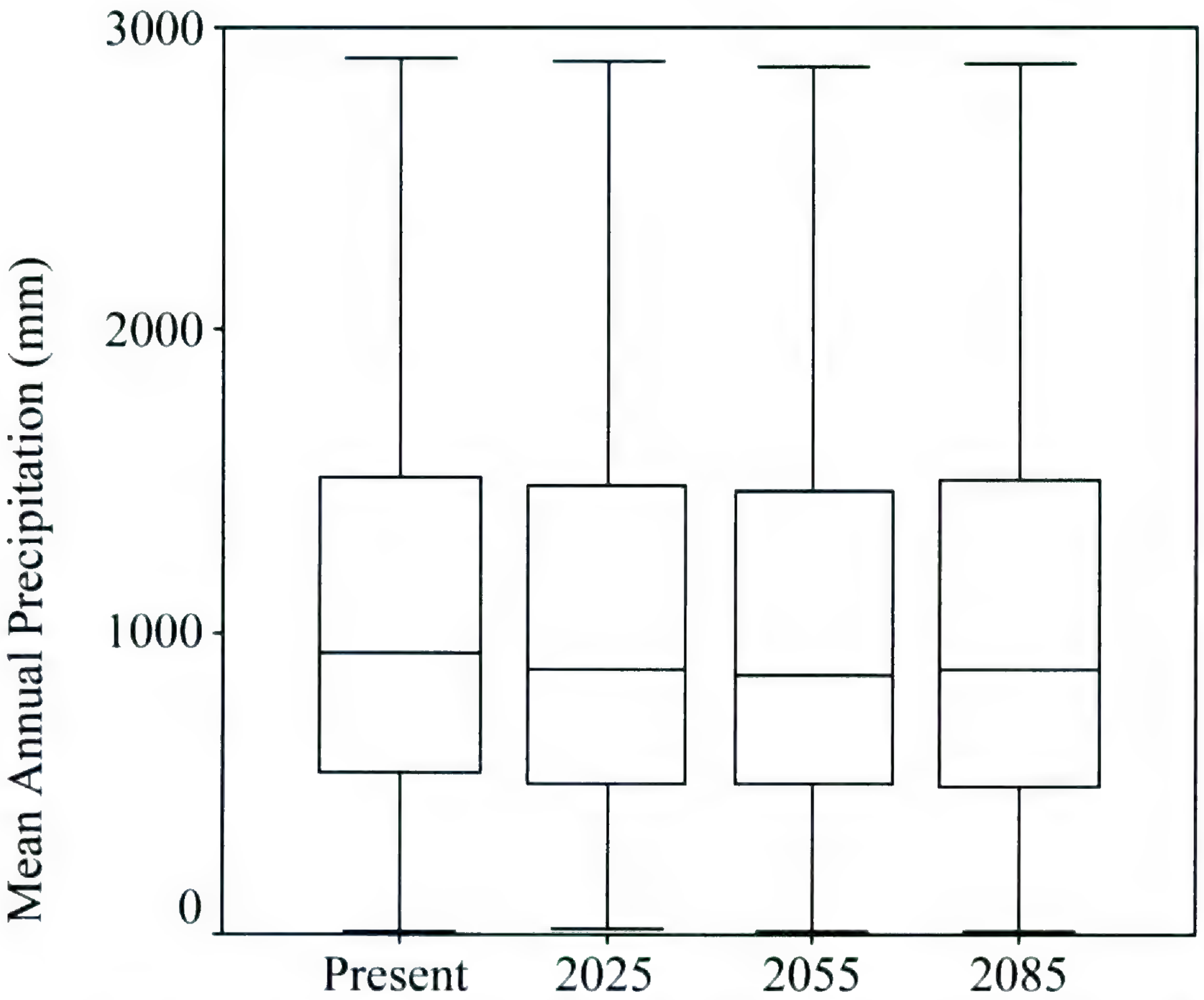

Figure 2. Box-plots of mean annual precipitation for grid cells detected as areas of suitable climate for each species under current predictions. Middle line in boxes gives median value for 5197 species. Upper line of box gives upper quartile, while lower line gives lower quartile. Whiskers extend over range after outliers and extremes have been removed. These results are for the BGA model.

Kenya begin to lose climatically suitable areas by 2025 in the SGA and BGA models (Fig. 3d, g). By 2085 the Western African Forests and the Succulent Karoo have lost much of their suitability for many species.

For the present predictions and the three future periods' predictions (full dispersal) we have calculated the average altitudes of the grid cells that contain suitable climate for each species. These average altitudes increase over each of the time periods modeled (Table 3, Fig. 4). The median altitude for species in 2085, for the conservative BGA model, is 178 m higher than the median for current predictions. However, even with full dispersal, spe-

Table 3. Numbers of species out of 5197 (percentages given in parentheses) predicted to increase and decrease climatically suitable area (full dispersal assumption) and lose all climatically suitable area (under two dispersal assumptions). The final row records the change in the median value of average elevations for climatically suitable areas from present predictions.

	BOX 2025	BOX 2055	BOX 2085	SGA 2025	SGA 2055	SGA 2085	BGA 2025	BGA 2055	BGA 285
Increasing climate suitability	616 (12%)	309 (6%)	146 (3%)	911 (18%)	571 (11%)	425 (8%)	1406 (27%)	1211 (23%)	994 (19%)
Decreasing climate suitability	4514 (87%)	4860 (94%)	5021 (97%)	4104 (79%)	4516 (87%)	4675 (90%)	3790 (73%)	3986 (77%)	4202 (81%)
Area lost (no dispersal)	1696 (33%)	2424 (47%)	2891 (56%)	2572 (49%)	3498 (67%)	3955 (76%)	1073 (21%)	1437 (28%)	1752 (34%)
Area lost (full dispersal)	1341 (26%)	1855 (36%)	2185 (42%)	1851 (36%)	2561 (49%)	2950 (57%)	768 (15%)	1007 (19%)	1298 (25%)
Increase in elevation (m)	152	239	343	173	294	390	111	137	178

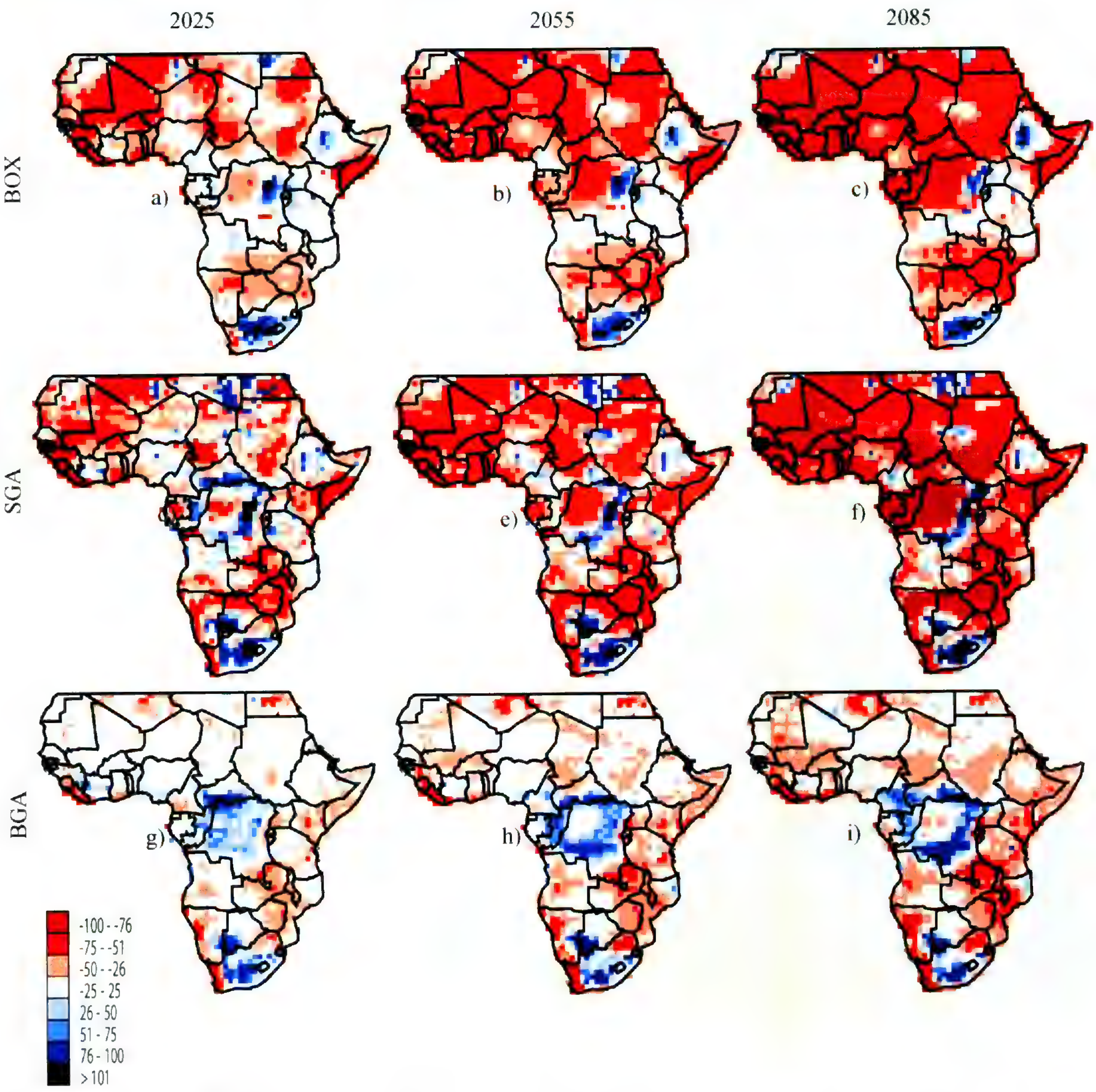

Figure 3. Percentage change in the number of species for which one-degree cells are climatically suitable between present predictions and future predictions.

cies are limited by fixed upper limits to elevation across Africa, as is demonstrated by the interquartile range of species' average altitudes becoming reduced as the lower quartile value increases in line with the median, while the upper quartile increases only marginally in later periods (Fig. 4).

Important temperature variable thresholds may also be squeezed in this way. For the BGA model we can, however, ascertain which climate variables are most influential in determining which areas are most suitable for a species. Across all of the species we study, the three most influential variables are annual precipitation, mean temperature of the warmest month, and annual moisture index (19.7%, 15.8%, 14.6% of species, respectively; Tables 1, 2). Our study of the changes in the climate variables over the study periods in the geographical areas that currently have suitable climate for the species (Figs. 1, 2) shows that across the sample species, on average, temperature variable values rise while precipitation-based variable values fall. However, the precipitation variable decreases are much less pronounced than the temperature variable increases and the variations across the sample for precipitation variables tend to be larger. This indicates that there is both substantial geographical complexity in such changes and that increasing temperature variables are likely to be the driving factors behind the shift of climatically suitable areas to higher altitudes.

Finally, we calculate an index of floristic turnover for each grid cell. For future climate predic-

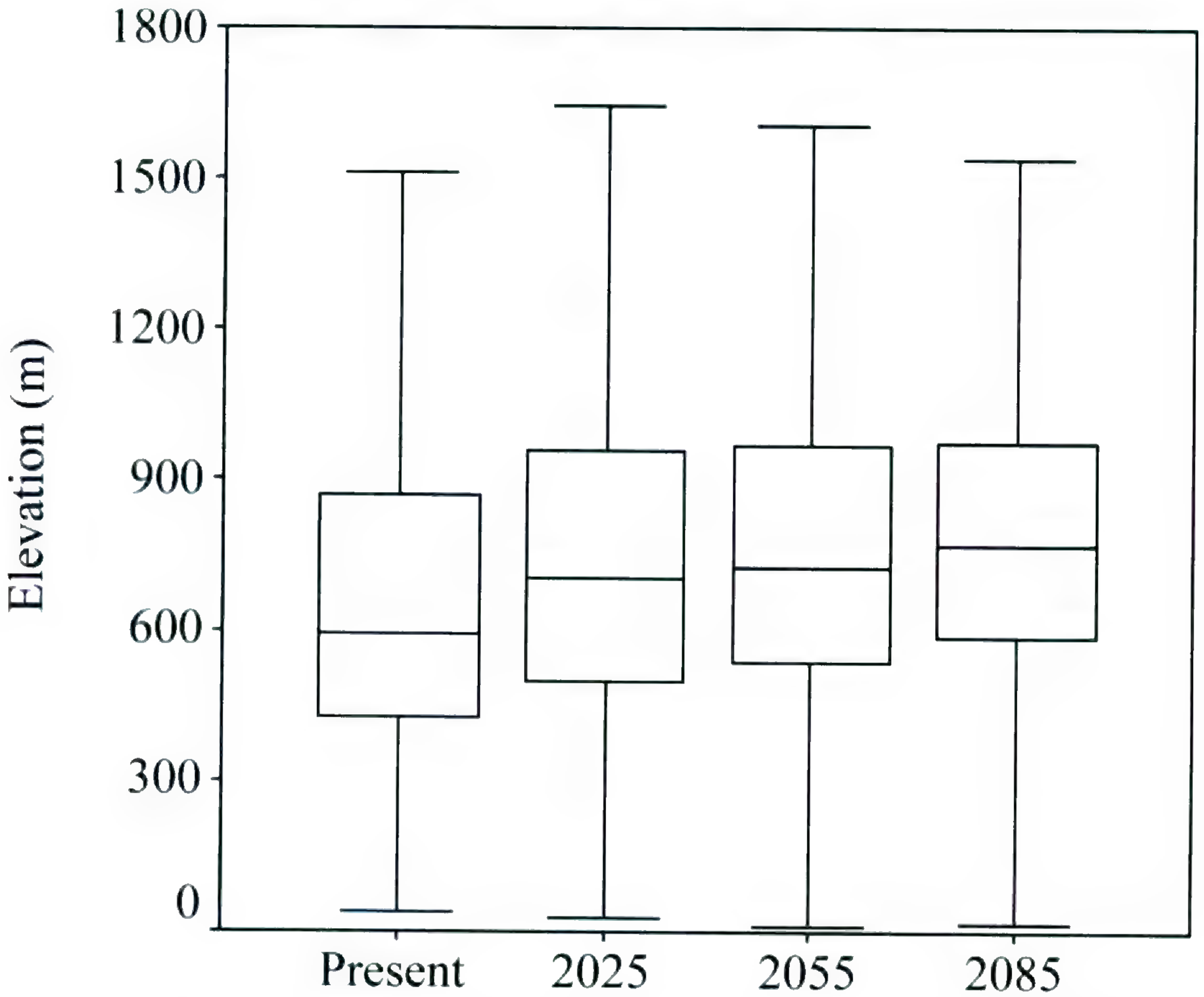

Figure 4. Box-plots of average elevation for climatically suitable areas for species in the four modeled time periods. Middle line in boxes gives median value for 5197 species. Upper line of box gives upper quartile, while lower line gives lower quartile. Whiskers extend over range after outliers and extremes have been removed. These results are for the BGA model.

tions, this takes into account how many species are left with suitable climate in a grid cell in relation to both the original number of species with suitable climate in that cell, and the number of species for which the cell becomes climatically suitable. A score of one suggests that there has been no change in the species for which the area is climatically suitable. A score of zero suggests that the area is no longer suitable for any of the original species. By 2085, most areas have an index of 0.5 or below, indicating that many areas have climate suitable for less than half the original species for which those areas were once suitable (Fig. 5a–i).

Discussion

In the discussion we first address shortcomings of the modeling methodology, in particular the risk of overemphasizing extinction rates. Second, we briefly review our findings in the context of past climate change, and finally we make suggestions that might be useful for implementation of the Global Strategy for Plant Conservation.

The modeling technique has two main limitations that may lead to an overestimation of the effects of climate change. Firstly, we assume that the presence of a plant species is solely determined by climate. In reality, the distribution of many plant species is in addition determined by, for example, competition, soil-type, fire, and micro-climates within structured vegetation. If other factors are suitable, species may have broader climatic tolerances than indicated by our model. Secondly, we are working at a scale of one degree. There can be high habitat heterogeneity within a one-degree cell and plants can survive periods of climatic extremes in small refugia. For example, many rainforest plants also occur in riverine or groundwater forests outside areas of continuous forest. Thus, when interpreting the results, it must be borne in mind that the model is showing extinction of potential climate-space (Table 3) rather than actual species extinctions. However, the model may also underestimate extinctions by not including factors such as fire. Africa has a long history of fire, with increases in fire episodes during switches of climate from interglacial to glacial, with a marked increase in fire during the present interglacial that is attributed to human influence (Bird & Cali, 1998). Drought and

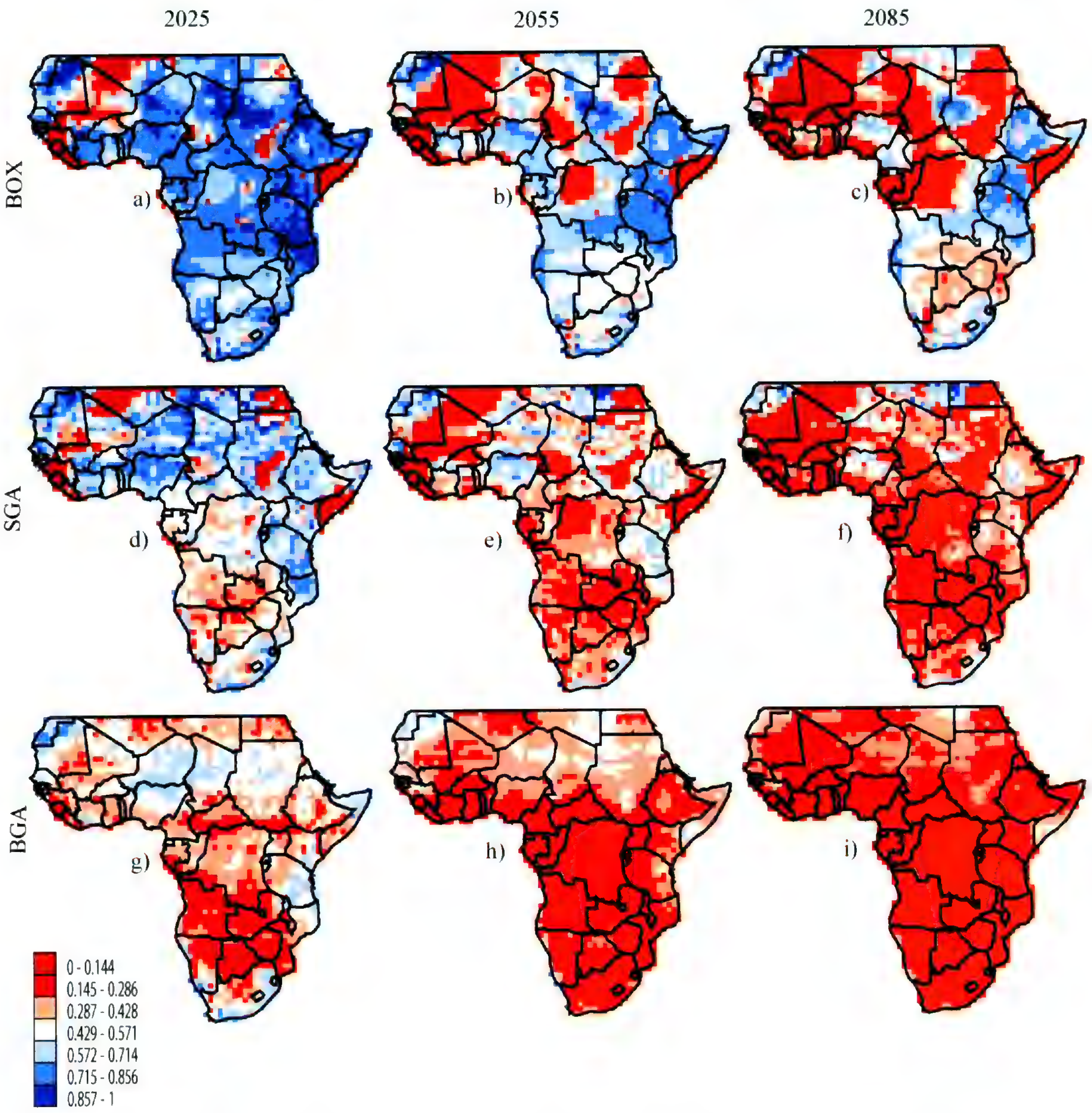

Figure 5. Maps of Sørensen's index showing climate niche turnover from present predictions to future predictions.

disturbance are implicated in enhanced extinction rates in fire-vulnerable formations such as rainforests throughout the tropics (Nepstad et al., 1999; Taylor et al., 1999; Cochrane, 2003) including Africa (Clarke & Karoma, 2000), and fire is considered to be a major determinant of global vegetation patterns (Bond et al., 2005). The preliminary estimates presented here need much further investigation of species responses to climate variability in an ecosystem context, including the effects of disturbance and human impacts. For example, pioneer forest has expanded along the northern boundary of the Guineo-Congolian forests (J. Maley, pers. comm.), an observation that runs counter to the trends modeled here.

From the assessments of kappa coefficients for the BOX and SGA models, it appears that as expected, the simple genetic algorithm approach gives better discrimination in terms of correctly predicting species presence observations and minimizing overpredictions for present climate. When the climate thresholds found by these models are projected into future climates, these models are likely to be very strict in their assessment of where suitable climates for a particular species might be located. The resulting patterns of change reflect the severity of the assumptions in this modeling approach. However, the broader climate envelopes produced by the BOX models show the areas that possess the combinations of climate variables where species presence has been observed. When these envelopes are projected onto future climate,

we at least obtain the areas under future climate that have been observed to possess the species at present. The magnitude of change in these predictions is still dependent on the assumption that if suitability in terms of one climate variable is lost, all suitability is lost.

The BGA approach overcomes the latter assumption by allowing the probability of species occurrence to be reduced, but not removed, if an area becomes less suitable in terms of one (or more) climate variables. The high AUC scores associated with these models gives us some confidence that the influence associated with each climate variable in these models is sensibly apportioned, and therefore probabilities of occurrence in the future may be more robust than the simple presence/absence predictions of the other methods.

Despite limitations of the modeling technique, the results bear some similarities with proposed effects of past climate change. Dynamism of the Guineo-Congolian forests in our model is consistent with palaeoecological information, which suggests that Central and West Africa have been subject to large changes in climate, species composition, and species diversity (Servant et al., 1993; Maley, 1996; Maley & Brenac, 1998; Nichol, 1999). For example, range expansion of the oil palm (*Elaeis guineensis* Jacq.) is considered to be associated with late Holocene forest decline around 2500 yrs BP (Maley & Chepstow-Lusty, 2001), and genetic diversity of the shea tree (*Vitellaria paradoxa* C. F. Gaertn.) appears to be associated with climatic changes at the Dahomey Gap such as increased aridity and expansion of this arid corridor during the last glacial maximum 15,000–20,000 yrs BP (Fontaine et al., 2004).

Elevational range in the Drakensberg was picked out by our model as important as a potential refugium for plant survival. Modern-day plant diversity is associated with areas of high topodiversity (Mutke et al., 2002). A possible reason for this is that these areas offer an adjacent range of habitats within which plants can move during periods of climate change. African biodiversity hotspots may owe their existence to persistence in refugia through Quaternary climatic fluctuations, which were both cooler and drier than at present (Hamilton, 1976, 1982; Maley, 1991, 1996, 2001a) and warmer (at 2500 and 125,000 yrs BP, Maley, 1996, 2001b). In our model, despite high floristic turnover and loss of suitable climate for many species, the results show montane areas gaining in suitable climate space for many species. Similar effects may pertain at finer scales than that of this study (Hannah et al., 2002a; Midgley et al., 2003). This supports recent suggestions that areas of topographic diversity are likely to be important climate change refugia and so should, a priori, be selected for conservation (SABONET, 2004), following previous advocacy of such policies for specific areas in Africa (Cowling & Pressey, 2001; Cowling et al., 2003). Our results suggest that areas of high terrain diversity could provide useful additions to current in situ conservation efforts and be important for meeting the GSPC goals in the face of potential future climate change.

Microclimates at finer scales than that of this study may provide refugia for small populations of individual species, while the loss of broad-scale climate suitability indicated here will result in major loss of area of occupancy and population reductions. These results suggest that under pressures of climate change, species composition in areas may change quite drastically, with potentially profound effects on ecosystem stability and the associated ecosystem goods and services utilized by the human population. Beyond 2085, our results suggest that meeting existing conservation targets may no longer be possible if current greenhouse gas emission patterns continue unabated. This is not only relevant to the GSPC. Article 2 of the 1992 UN Framework Convention on Climate Change (UNFCCC) aims to reduce human-induced climate change to a level that will allow ecosystems to naturally adapt to climate change. Greater inter-agreement communication and greater recognition of the sensitivity of biodiversity to climate change seem necessary for both the CBD and UNFCCC to achieve their goals. Our work demonstrates that there may be great pressure on species to shift their ranges in response to changing environments. The rates at which species may be required to accomplish such shifts are likely to be determined by actions taken under the UNFCCC. Our results suggest that time is running out; climate change abatement strategies may be too slow to avoid many species losing major proportions of the areas that are climatically suitable for them. This and the associated potential changes in species composition have major implications for signatories to the CBD as they seek to establish systems of protected areas that will maintain plant species diversity.

In conclusion, we would like to emphasize the importance of primary data collection in the field. We are indebted to all those responsible for recording distribution data in monographs and preserving collections in herbaria. Our modeling work is dependent on such collections, and future recording efforts will continue to be essential for the successful implementation of the GSPC.

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JUMPING GENERA: THE PHYLOGENETIC POSITIONS OF *CASSYTHA*, *HYPODAPHNIS*, AND *NEOCINNAMOMUM* (LAURACEAE) BASED ON DIFFERENT ANALYSES OF *trn*K INTRON SEQUENCES[1]

Jens G. Rohwer[2] *and Barbara Rudolph*[2]

ABSTRACT

Since earlier investigations gave conflicting results, we re-examined the phylogeny of the Lauraceae with an enlarged data set from the *trn*K intron, including a higher number of critical taxa and a larger number of coding (*mat*K) and non-coding sequence positions. The source of earlier conflicts was explored by using different algorithms (parsimony, maximum likelihood, and Bayesian inference), different taxon samples (by exclusion of one or two of the critical taxa), and different parts of the matrix (entire *trn*K intron, coding or non-coding positions only). The results suggest that (1) Bayesian inference (and in smaller data sets also maximum likelihood) yields results that are more consistent with the distribution of informative indels than the results of parsimony analyses, (2) the monotypic African genus *Hypodaphnis* is sister to all other Lauraceae, (3) *Neocinnamomum* is indeed close to *Caryodaphnopsis*, as morphology would suggest, and (4) the parasitic genus *Cassytha* is not sub-basal, as in our earlier analysis, but nested among the otherwise woody Lauraceae as sister group to a clade including all genera except *Hypodaphnis* and the Cryptocarya group.

Key words: Bayesian inference, *Cassytha*, *Hypodaphnis*, Lauraceae, *mat*K, *Neocinnamomum*, phylogeny, *trn*K intron.

With an estimated 2500–3500 species (Rohwer, 1993), the Lauraceae are the largest family of woody magnoliid angiosperms. In moist and wet tropical forests of America, Asia, and Australia, they are usually among the 12 most frequent families (Gentry, 1988), often becoming (co-)dominant in montane forests. Even in Africa they may be among the most frequent families, although they are less diverse there. Relatively few species occur in temperate forests, as far north as Ontario (Canada) or Hokkaido (Japan), and as far south as Chiloe Island (Chile) or New Zealand. In the Northern Hemisphere, the family has a well-documented fossil record from the early mid-Cretaceous onward (Drinnan et al., 1990; Crane et al., 1994; Herendeen et al., 1994; Eklund & Kvaček, 1998; Takahashi et al., 1999; Eklund, 2000, and references cited therein), whereas fossil evidence from the Southern Hemisphere is rare (e.g., Poole et al., 2000) or questionable prior to the Eocene.

After decades of controversy about the relationships within the family (see van der Werff & Richter, 1996), the first study using a molecular marker (Rohwer, 2000) suggested an entirely novel model for the phyletic lines. A more comprehensive study using several different markers (Chanderbali et al., 2001) yielded largely congruent results. However, the two studies differed considerably in (1) the taxon sample, (2) the number of informative mutations in the two data sets (169 vs. up to 684), and (3) the placement of the aberrant parasitic genus *Cassytha*. The position of this genus has been contro-

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[2] Biozentrum Klein Flottbek und Botanischer Garten, Universität Hamburg, Ohnhorststr. 18, 22609 Hamburg, Germany. rohwer@botanik.uni-hamburg.de

versial throughout the history of the Lauraceae. The extremes ranged from separation as a family of its own (Lindley, 1836) to inclusion in the Cryptocarya group (Rohwer, 1993). In the first molecular study (Rohwer, 2000), *Cassytha* was resolved as sister group to all Lauraceae except the aberrant African genus *Hypodaphnis*, whereas in the second study (Chanderbali et al., 2001) it was nested within the Lauraceae, as sister to the Asian genus *Neocinnamomum*, which had not been included in the first study. Therefore, we expanded our original matrix by an approximate doubling of the sequence length considered in order to obtain more stable results. In addition, the taxon sample was changed to include a larger number of taxa belonging to other families of the Laurales and to the (presumably) more basal clades within the Lauraceae. On the other hand, we reduced the size of the extremely closely knit terminal group (called the "Perseeae–Laureae clade" by Chanderbali et al., 2001) that was identified in both of the earlier analyses. We also produced a simplified matrix (see below) that allowed assessments of the influence of different taxon samples, different partitions of the matrix, and different methods of analysis. With these experiments, we tried to address the following questions: Was the conflict between the earlier analyses caused by the different taxon sample? If so, which taxa are responsible for the differences? Are some methods of analysis more sensitive to changes in the taxon sample than others? Are the results from coding and non-coding parts of the matrix congruent? If not, why not?

Materials and Methods

Choice of Outgroup

In order to assess the monophyly of the Lauraceae, especially with respect to the rather aberrant genera *Cassytha* and *Hypodaphnis*, seven species from four other lauralean families (Atherospermataceae, Calycanthaceae, Hernandiaceae, and Monimiaceae, see Table 1) were included in the analysis. This made it necessary to select a non-lauralean family as an outgroup. Most recent analyses (e.g., Mathews & Donoghue, 2000; Qiu et al., 2000; Hilu et al., 2003) suggest that the Magnoliales are sister to the Laurales, and a database search (via fasta@ebi.ac.uk) retrieved *trn*K intron sequences of Magnoliaceae as the closest match to those of different Laurales. Therefore, three species of the Magnoliaceae (see below) were chosen as outgroup.

Taxon Sampling

Much of the material examined here is the same as in our earlier publication (Rohwer, 2000). However, several taxa from the largely unresolved terminal group and a few from the Persea group were excluded because of very low sequence divergence. In addition, we had to exclude *Cryptocarya triplinervis* and *Caryodaphnopsis tonkinensis* because our DNA sample was insufficient for amplification of the missing fragment and due to sequencing problems, respectively.

On the other hand, we added a number of taxa (Table 1) that were not available at the time of our first analysis (Rohwer, 2000). Many of them (*Anaueria brasiliensis*, *Aspidostemon parvifolium* and an unidentified *Aspidostemon* species, *Eusideroxylon zwageri*, *Neocinnamomum mekongense*, *Potameia chartacea*, and *Sextonia rubra*) belong to genera of the Lauraceae that were not represented in the first matrix, but were shown to fall outside the terminal group by Chanderbali et al. (2001). Other species (*Caryodaphnopsis bilocellata*, *Caryodaphnopsis tomentosa*, *Cassytha melantha*, *Cassytha pubescens*, and *Chlorocardium venenosum*) were added with the expectation that they would reduce long-branch effects by breaking up the often rather long branches that led to the only representative of these genera in the first analysis. In the genera *Beilschmiedia* and *Endiandra*, further species were added in order to check whether *Endiandra* was indeed nested within *Beilschmiedia*, as it appeared from both of the earlier analyses, albeit with weak support. Finally, two species were added that could be expected to fall within the terminal group, *Actinodaphne diversifolia* and *Ocotea malcomberi*, both representatives of genera that are suspected of being polyphyletic (Li et al., 2004; Chanderbali et al., 2001).

DNA Extraction

Total genomic DNA was isolated from leaves of fresh, silica-gel dried, or herbarium material. Up to 60 mg of fresh leaves or about 20 mg dried material were ground either with liquid nitrogen in a mortar or with sea sand and a microhomogenizer. The choice of method depended on the stability as well as the amount of available material. DNA was extracted according to Dumolin et al. (1995), with some modifications, or using commercial kits such as DNeasy Plant Mini Kit (Qiagen), Invisorb Spin Plant Mini Kit (Invitek), or NucleoSpin Plant Kit (Macherey-Nagel). DNA isolations via commercial kits were performed according to the manufacturer's instructions, with slight modifications as provided

below. Directly after cell lysis incubation, the suspension was centrifuged for 1 minute at 13,000 rpm (Biofuge fresco, Kendro Laboratory Products GmbH) to pellet the mixture of sand and cell fragments. The clear supernatant was applied to the spin column. To elute the bound DNA, 50 µl elution buffer was added to the spin column, incubated for 5 minutes, and centrifuged according to the manual's instructions. To increase the amount of eluted DNA, this step was repeated once using a separate reaction tube. The quality and quantity of isolated DNA was checked visually by gel electrophoresis on a 0.8% agarose gel in 0.5x TBE and ethidiumbromide staining.

The extraction according to Dumolin et al. (1995) was modified as follows: cell lysis was carried out through incubation with 950 µl extraction buffer and 50 µl 1 M DTT at 65°C for 10 minutes. After cooling down to room temperature, 400 µl dichlormethane was added, mixed carefully, and centrifuged (5 min., 4°C, 10,000 rpm.). To precipitate DNA, the upper phase was transferred into a new tube and mixed with ⅔ X volume isopropanol. The final centrifugation step (10 min., 4°C, 13,000 rpm.) followed without incubation. The supernatant was removed and the pellet was washed in 500 µl 76% ethanol. The DNA was dried at 65°C for about 5 minutes and resuspended in 50 µl TE. To allow the DNA to dissolve completely, the sample was stored at 4°C for at least one week before further utilization.

AMPLIFICATION

The *trn*K intron (ca. 2500 bp) including the *mat*K gene was amplified by standard polymerase chain reaction (PCR) between the primers 3914 and *trn*K-II of Steele and Vilgalys (1994). Usually 2 µl DNA solution (occasionally less or more, depending on the DNA concentration) was used as template in a 10 µl PCR reaction including 1x Taq buffer, 5 mM $MgCl_2$, 200 µM dNTPs, and 0.25 u Taq DNA Polymerase (GeneCraft). Because frequently only short fragments of less than 500 bp could be amplified from herbarium material, it was necessary to design a number of internal primers (Table 2) for this study. The reactions were performed using a Biometra T Gradient or T Personal thermocycler, under the following conditions: 95°C for 4 minutes, 30 cycles at 95°C for 45 seconds, 52°C for 45 seconds, and 72°C for 1 minute (for short fragments) or 3 minutes (for fragments longer than 600 bp), plus a final extension step at 72°C for 5 minutes. The amplification products were separated on an agarose gel under the same conditions as above. The PCR products were purified using commercial purification kits (Montage PCR, Millipore; NucleoSpin Extract 2 in 1, Macherey-Nagel). In some cases, when the PCR yielded more than a single product, the DNA was separated via 0.8% agarose gel electrophoresis in 1x TAE. The fragment of the appropriate size (which usually formed the strongest band on the gel) was cut out and purified via the Qiaquick Gel Extraction Kit (Qiagen). The quality and quantity of purified PCR product was checked against a reference of known concentration using agarose gel electrophoresis.

SEQUENCING

Cycle sequencing reactions in both directions were performed using BigDye (Applied Biosystems) according to manufacturer's instructions with aliquots of the purified PCR products (amount depending on the DNA concentration) and one of the PCR primers (Table 2). The sequencing reaction products were separated using an ABI Prism 3770 Capillary Sequencer (Applied Biosystems) at the University Hospital Eppendorf (UKE, Hamburg), Institute of Cell Biochemistry and Clinical Neurobiology.

SEQUENCE ALIGNMENT

To transfer the sequence data to the alignment program Sequencher™ 3.1.1 (GeneCodes), the file had to be converted via BioEdit Sequence Alignment Editor (Department of Microbiology, North Carolina State University). The different sequence fragments of any one taxon were aligned automatically in Sequencher, and then checked manually. The fully edited sequences, generally confirmed by forward and reverse sequencing reactions, were deposited in EMBL under the accession numbers indicated in Table 1. In addition, sequences of *Liriodendron tulipifera* L. (AB021017), *Michelia figo* Spreng. (AB021015), and *Magnolia macrophylla* Michx. (AB020997), as well as partial sequences of *Dodecadenia grandiflora* Nees (AF244409), *Gyrocarpus americanus* Jacq. (AF465295), *Iteadaphne caudata* (Nees) H. W. Li (AF244408), and *Parasassafras confertiflora* (Meisn.) D. G. Long (AF244392) were retrieved from EMBL. The sequences of different taxa were aligned manually. In the coding region, this was possible without any problems (see results). In the two spacer regions, on the other hand, a relatively high number of indels had to be inserted, most of them simple duplications of adjacent motifs. However, in some cases different alignments appeared possible. If one of them would make a character informative that was

Table 1. Material examined.

Taxon	Voucher	Provenance	EMBL No.
Actinodaphne borneensis Meisn.	*Atkins 450* (AAU)	Brunei	AJ247142
Actinodaphne diversifolia Merr.	*Dransfield 7467* (L)	Brunei	AJ627910
Alseodaphne perakensis (Gamble) Kosterm.	*van Balgooy 2186* (HBG)	Malaysia	AJ247144
Anaueria brasiliensis Kosterm.	*Vásquez 25228* (MO)	Peru	AJ627911
Aniba affinis (Meisn.) Mez	*Ziburski 547* (HBG)	Bot. Gard. Bonn	AJ247145
Apollonias barbujana (Cav.) Bornm.	*Rohwer 151* (MJG) 323-90	Bot Gard. Bonn	AJ247146
Aspidostemon parvifolium (Scott-Elliot) van der Werff	*Lowry 5024* (MO)	Madagascar	AJ627912
Aspidostemon sp. indet.	*van der Werff 12765* (MO)	Madagascar	AJ627913
Beilschmiedia berteroana (Gay) Kosterm.	*Zöllner 21411* (HBG)	Chile	AJ247147
Beilschmiedia brenesii C. K. Allen	*van der Werff 14015* (MO)	Costa Rica	AJ627914
Beilschmiedia madagascariensis (Baill.) Kosterm.	*Lowry 5015* (MO)	Madagascar	AJ627915
Beilschmiedia mexicana (Mez) Kosterm.	*Reyna 1404* (HBG)	El Salvador	AJ247148
Beilschmiedia miersii (Gay) Kosterm.	*Greissl 657-99* (MJG)	Chile	AJ627916
Beilschmiedia roxburghiana Nees	*Gerlach s.n.* (MJG)	Bot. Gard. Munich	AJ247149
Beilschmiedia tawa (A. Cunn.) Kirk	*Chase 5519* (K)	Bot. Gard. Kew	AJ247150
Calycanthus occidentalis Hook. & Arn.	*Rohwer s.n.* (HBG)	Bot. Gard. Hamburg	AJ627917
Caryodaphnopsis bilocellata van der Werff & N. K. Dao	*van der Werff 14195* (MO)	Vietnam	AJ627918
Caryodaphnopsis tomentosa van der Werff	*Neill 10134* (MO)	Ecuador	AJ627919
Cassytha ciliolata Nees	*Rohwer 175* (MJG)	Bot. Gard. Mainz	AJ247152
Cassytha melantha R. Br.	*Felger s.n.* (HBG)	Bot. Gard. Marburg	AJ627920
Cassytha pubescens R. Br.	*Röser et al. 10847* (LZ)	Australia	AJ627921
Chlorocardium rodiei (R. H. Schomb.) Rohwer, H. G. Richt. & van der Werff	*Polak 281* (HBG)	Guyana	AJ247153
Chlorocardium venenosum (Kosterm. & Pinkley) Rohwer, H. G. Richt. & van der Werff	*Vásquez 25236* (MO)	Peru	AJ627922
Cinnamomum camphora (L.) J. Presl	*Rohwer 164* (MJG)	Bot. Gard. Mainz	AJ247154
Cryptocarya alba (Molina) Looser	*Chase 5521* (K)	Bot. Gard. Kew	AJ247158
Cryptocarya subtriplinervia (Kosterm.) van der Werff	*van der Werff 12755* (MO)	Madagascar	AJ627923
Dehaasia cuneata (Blume) Blume	*de Wilde 12742* (HBG)	Sumatra	AJ247160
Endiandra impressicosta C. K. Allen	*Gray 7539* (MO)	Australia	AJ627924
Endiandra kingiana Gamble	*Ambri & Arifin W 763* (L)	Borneo	AJ627925
Endiandra pubens Meisn.	*Constable 4876* (HBG)	Australia	AJ247162
Endlicheria verticillata Mez	*Vásquez 9123* (AAU)	Peru	AJ247164
Eusideroxylon zwageri Teijsm. & Binn.	*Gwee, SING 2004-42* (SING)	Bot. Gard. Singapore	AJ627926
Hedycarya arborea J. R. Forst. & G. Forst.	*Rohwer s.n.* (HBG)	Bot. Gard. Hamburg	AJ627927
Hernandia nymphaeifolia (C. Presl) Kubitzki	*Rohwer 166* (MJG)	Bot. Gard. Mainz	AJ247165
Hypodaphnis zenkeri (Engl.) Stapf	*Leeuwenberg 5557* (HBG)	Cameroon	AJ247166
Laurelia sempervirens (Ruiz & Pav.) Tul.	*Greissl 643-99* (MJG)	Chile	AJ627928
Laurus azorica (Seub.) Franco	*Rohwer 168* (MJG)	Bot. Gard. Mainz	AJ247167
Licaria triandra (Sw.) Kosterm.	*Zona s.n.* (FTG)	Miami, FTG #X-1-172	AJ247168

Table 1. Continued.

Taxon	Voucher	Provenance	EMBL No.
Lindera benzoin (L.) Blume	*Rohwer 170* (MJG)	Bot. Gard. Mainz	AJ247169
Mezilaurus opaca Kubitzki & van der Werff	*Revilla 1226* (HBG)	Peru	AJ247172
Nectandra coriacea (Sw.) Griseb.	*Zona s.n.* (FTG)	Miami, FTG # X-4-50	AJ247173
Neocinnamomum mekongense (Hand.-Mazz.) Kosterm.	*Li Heng 8547* (MO)	China	AJ627935, AJ627932
Ocotea foetens (Aiton) Baill.	*Rohwer 157* (MJG)	Bot. Gard. Bonn 575-90	AJ247177
Ocotea malcomberi van der Werff	*van der Werff 12576* (MO)	Madagascar	AJ627929
Ocotea paulii C. K. Allen	*Gomez-Laurito s.n.* (HBG)	Costa Rica	AJ247178
Persea americana Mill.	*Rohwer 181* (MJG)	Bot. Gard. Mainz	AJ247179
Persea grijsii (Hance) Kosterm.	*Rohwer 163* (MJG)	Bot. Gard. Hamburg	AJ247180
Persea indica (L.) Spreng.	*Rohwer 172* (MJG)	Bot. Gard. Mainz	AJ247181
Peumus boldus Molina	*Rohwer 182* (MJG)	Bot. Gard. Hamburg	AJ247183
Potameia chartacea Kosterm.	*van der Werff 12835* (MO)	Madagascar	AJ627930
Sassafras tzumu (Hemsl.) Hemsl.	*Rohwer 160* (MJG)	Bot. Gard. Bonn 3991	AJ247188
Sextonia rubra (Mez) van der Werff	*Projeto Ducke 1223* (MO)	Brazil	AJ627933, AJ627934
Sparattanthelium amazonum Mart.	*Hammel 22270* (MO)	Costa Rica	AJ627931
Tambourissa religiosa (Tul.) A. DC.	*Kramer s.n.* (MJG)	Bot. Gard. Heidelberg	AJ247189
Umbellularia californica (Hook. & Arn.) Nutt.	*Rohwer 173* (MJG)	Bot. Gard. Mainz	AJ247190
Wilkiea huegeliana (Tul.) A. DC.	*Röser et al. 10989* (LZ)	Australia	AJ627932
Williamodendron glaucophyllum (van der Werff) Kubitzki & H. G. Richt.	*Burger 12348* (HBG)	Costa Rica	AJ247192

⟨http://www.ebi.ac.uk/embl/index.html⟩

Table 2. Sequences of internal primers used in this study.

Lab name	Position	Sequence (5′ → 3′)
A1 F	337	AAT TCG AAT GAT TAC CCG AT
A2 R	423	GAT CCA ATA ACA AGA GAA CC
PT1 R	434	AAA GGA ATY GAT GAT CCA CT
PT2 F	460	TTT TTT CAT GAA TCC TAA CT
A3 F	947	TAT CTA CGC RCT TGC TCA TG
B4 R	1020	GTG AAC TGG ATT TAT TGT C
460 F	1326	GTG TCA GAT ATA CTA ATA CC
469 R	1326	GGT ATT AGT ATA TCT GAC AC
518 R	1384	AGY ATC TTG TAT CCA AGA GT
569 R	1430	TTC CAA TAC TCG TAG AGA
796 F	1692	ACC CTA TGG TTG TTC AAA GAC
Lau1 R	1692	GTC TTT GAA CAA CCA TAG GGT
870 R	1766	TCT TTA TCA GAA GAN GAG CC
958 R	1828	CCG GTT GAG ACC ACA AGT
Lau3 F	1972	CTA TTA AGA AAT TCG AGA CC
Lau4 R	2053	ACG GCT TAC TAA TGG GAT GCC
Lau5 F	2205	TGT GCT AGA ACT TTG TCT CG
Lau6 R	2309	TTG GGA AGA TCA AAG AAA GA

uninformative in the alternative, we selected the uninformative alignment in order to exclude potential artifacts. If both alternative alignments yielded different potential synapomorphies, the positions involved were excluded from the analysis. Additionally, all positions in which representatives of more than one genus had a gap were excluded from the analysis, but positions were not excluded where only the Magnoliaceae had a gap compared to the ingroup taxa. The remaining gaps were treated as missing data, as were positions for which the sequence could not be obtained (see results). When two or more taxa turned out to be identical in the sequence fragment analyzed, only one of them was included in the phylogenetic analysis. The final alignment is available from EMBL (ALIGN_000847) and from the authors.

PHYLOGENETIC ANALYSIS

Parsimony analyses were conducted as heuristic searches using PAUP* 4.0b10 (D. L. Swofford, Florida State University, Sinauer, Sunderland, Mas-

sachusetts; see also Swofford, 1993), with 100 random stepwise additions and the options COLLAPSE, MULTREES, and TBR. Bootstrap analyses (and jackknife analyses with 50% deletion for the largest possible matrix, see below) were performed with 100 replicates, each with 100 random stepwise additions. In cases when these ran into overflow during branch swapping (see below), with more than 65,000 equally parsimonious trees, MAXTREES was set to 5000 in the final analyses. Fast bootstrap analyses with 10,000 replicates, but without branch swapping (Mort et al., 2000), were performed on the matrices including the complete taxon sample (see below), either in addition to the standard bootstrap and jackknife analyses (full matrix) or to replace them (in analyses of only the coding or the non-coding regions).

In order to test the influence of different taxon samples (by exclusion of certain taxa), different partitions of the matrix (coding, non-coding, both combined), and different methods of analysis (parsimony, maximum likelihood, Bayesian inference), we created a second, simplified matrix. This was achieved by creating majority consensus sequences from those taxa that were members of a group which (a) received 99% or 100% support (bootstrap, jackknife, and/or fast bootstrap) in the parsimony analysis and 100% posterior probability in the Bayesian analysis (see below) of the complete matrix, and (b) was so tightly knit that the maximum number of differences among its members was up to half the minimum number of differences between a member and a non-member.

In order to detect long-branch attraction, taxon deletion experiments were performed with the three genera of Lauraceae that showed the longest branches in an unrooted distance tree (absolute number of differences, star decomposition search, Fig. 1). In the first step, one of these taxa at a time was deleted. If any of the three initial deletions led to a conflicting topology, either two of the three taxa were deleted in a second step (see Table 4, e.g., No. 16–22).

For the maximum likelihood and the Bayesian inference analyses, the most appropriate substitution models for the coding and the non-coding regions were chosen by analyzing the respective parts of the matrix separately through ModelTest 3.06 (Posada & Crandall, 1998; see also http://inbio.byu.edu/Faculty/kac/crandall_lab/modeltest.htm). Maximum likelihood analyses were performed with PAUP separately for the coding and the non-coding sequences, using the parameters suggested by ModelTest according to the hierarchical likelihood ratio test (Table 3). Since bootstrap analyses using maximum likelihood as the optimality criterion proved very time-consuming, they were omitted in the taxon deletion experiments if there was no change in topology compared to the complete taxon sample.

For the Bayesian inference of phylogeny (using MrBayes 3.0B4; Huelsenbeck, 2000; Huelsenbeck & Ronquist, 2001; Ronquist & Huelsenbeck, 2003; see also http://morphbank.ebc.uu.se/mrbayes/manual.php) the data were separated into five unlinked partitions, two for the non-coding regions before and after the *mat*K gene, and one for each of the three codon positions of *mat*K. The rate matrices retrieved from ModelTest (Table 3) were specified as priors for the analysis. In the final analyses of the full matrix, four simultaneous MCMC chains were run for 1,000,000 generations, with the current tree saved every 100 generations. Of the 10,001 trees retrieved, the first 1000 (= 100,000 generations) were discarded as burnin, since the chain (when using the largest matrix) needed about 40,000 (coding region) to 80,000 (full matrix) generations to become stationary. The same parameters were used for a test run of the simplified matrix, which showed that setting these parameters almost an order of magnitude lower (100,000 generations, discarding the first 15,000) was sufficient, because the chain became stationary after 4500 (coding region) to 12,000 (full matrix) generations. Since MrBayes 3.0B4 only permits using a single taxon as an outgroup, we excluded *Magnolia* and *Michelia* in the Bayesian analysis of the complete matrix.

In total, 47 different phylogenetic analyses were performed (Table 4) based on the present *trn*K intron data. Support values (bootstrap, fast bootstrap, and jackknife support or posterior probabilities) of less than 50% are described as no support, whereas 50%–69% are considered as weak, 70%–89% as moderate, and 90%–100% as strong. After the analyses, MacClade 4.0 PPC was used to map informative indels that had been excluded earlier (see above) upon the phylogenetic trees obtained from the analyses, as a second, independent line of evidence. The same software was used to trace characters that supported unexpected clades.

Results

Sequence Lengths

Complete *trn*K intron sequences (between the primers 3914 and *trn*K-II of Steele & Vilgalys, 1994) were obtained for nearly all of the species indicated in Table 1, except for *Neocinnamomum mekongense* and *Sextonia rubra*. The alignment positions 462 to 951, and 2004 to 2082, respectively,

could not be amplified from the relatively poor herbarium material, despite numerous attempts. In the other species, the lengths of the analyzed sequences varied between 2457 bp in *Calycanthus occidentalis* and 2510 bp in *Sparattanthelium amazonum*.

ALIGNMENT

In the coding region, five deletion events, none of them between complete codons, and five insertion events, all of them simple duplications of adjacent motifs between complete codons, had to be postulated. The deletion events involved 6 bp common to *Beilschmiedia brenesii* and *B. mexicana*, 6 bp in different positions in *Calycanthus occidentalis*, *Chlorocardium venenosum*, and *Eusideroxylon zwageri*, and 27 bp in *Hernandia nymphaeifolia*. The duplications involved 12 bp in *Hernandia nymphaeifolia*, 6 bp in different positions in *Neocinnamomum mekongense*, *Peumus boldus*, and *Sparattanthelium amazonum*, plus an additional 3 bp in *Peumus boldus*. In addition, *Hernandia nymphaeifolia* was found to have a deletion of 5 bp, spanning the area where the stop codon (TGA) was found in other species. Because of the resultant frame shift, the coding region in this species extended 15 bp beyond that in the others, before it ended at a TAA codon. In the two species of *Caryodaphnopsis*, the stop codon was replaced by a GAA (Glu) codon, so that the *mat*K sequence ended at a TAG codon 24 bp further downstream. Although the original stop codon was retained, the *mat*K reading frame in *Neocinnamomum* ended one codon earlier than in the other species, because the penultimate codon (usually TTA) has been replaced by an additional stop (TAA) codon. Due to the insertion of gaps, the final alignment was 2750 bp long, of which 318 were excluded from the analysis because of gaps or uncertain alignment (see above). In the remaining 2432 alignment positions, none of the taxa was completely identical. Sequence divergence ranged from 1 bp between *Beilschmiedia berteroana* and *Beilschmiedia miersii* to 321 bp between *Cassytha ciliolata* and *Hernandia nymphaeifolia*. The complete matrix, containing all taxa and both coding and non-coding sequence regions, consisted of 64 taxa and 2432 non-excluded characters.

PHYLOGENETIC ANALYSES

None of the analyses performed could make use of the complete matrix, as the sequences retrieved from EMBL for *Dodecadenia grandiflora*, *Gyrocarpus americanus*, *Iteadaphne caudata*, and *Parasassafras confertiflora* covered slightly less than the coding region of the *mat*K gene. Therefore, these taxa were excluded from all analyses that involved the non-coding regions. In analyses of only the coding region (not shown), *Gyrocarpus americanus* came out as sister to *Sparattanthelium amazonum* (both Hernandiaceae), with 100% fast bootstrap support (FBS) and posterior probability (PP). *Dodecadenia* was weakly supported as sister to *Laurus* (63% FBS, 54% PP). The two remaining taxa (*Iteadaphne* and *Parasassafras*) were retrieved as members of a large basal polytomy in the Laureae–Cinnamomeae.

The largest possible matrix (i.e., containing all taxa except the four mentioned above and both coding and non-coding sequence positions, henceforth called "complete large matrix") consisted of 60 taxa and 2432 characters, of which 1411 were constant, 398 variable but parsimony-uninformative (henceforth called "uninformative"), and 623 informative. As *Beilschmiedia berteroana* and *B. miersii* differ only by a single base pair within the coding region, one sequence was taken to represent both of them when only the non-coding intron regions were considered. The "non-coding large matrix" therefore consisted of 59 taxa and 914 characters, of which 530 were constant, 163 uninformative, and 221 informative. When only the coding positions were considered, on the other hand, it was possible to include the five taxa mentioned above, so that the "coding large matrix" consisted of 64 taxa and 1518 characters, of which 867 were constant, 237 uninformative, and 414 informative.

Reducing the number of taxa as outlined in "Materials and Methods" led to a simplified matrix of 21 taxa and 2727 characters. The alignment became shorter than in the complete matrix (2750 bp, see above) because autapomorphic insertions occurring only in a few taxa within larger groups were no longer present in the majority consensus. Again *Gyrocarpus americanus* was excluded from analyses involving non-coding sequence positions. Therefore, the "complete simplified matrix" consisted of 20 taxa and 2727 characters, of which 292 were excluded because of gaps or uncertain alignment. Of the remaining 2435 characters, 1519 were constant, 554 uninformative, and 362 informative. The respective values for the coding and non-coding simplified matrices are 21/20 taxa and 1518/917 non-excluded characters, among those 930/580 constant, 348/202 uninformative, and 240/135 informative.

The topologies resulting from the 47 different analyses (Table 4) can be sorted into five groups (Fig. 2) that are incompatible with one another in their fully resolved form. However, the result of an

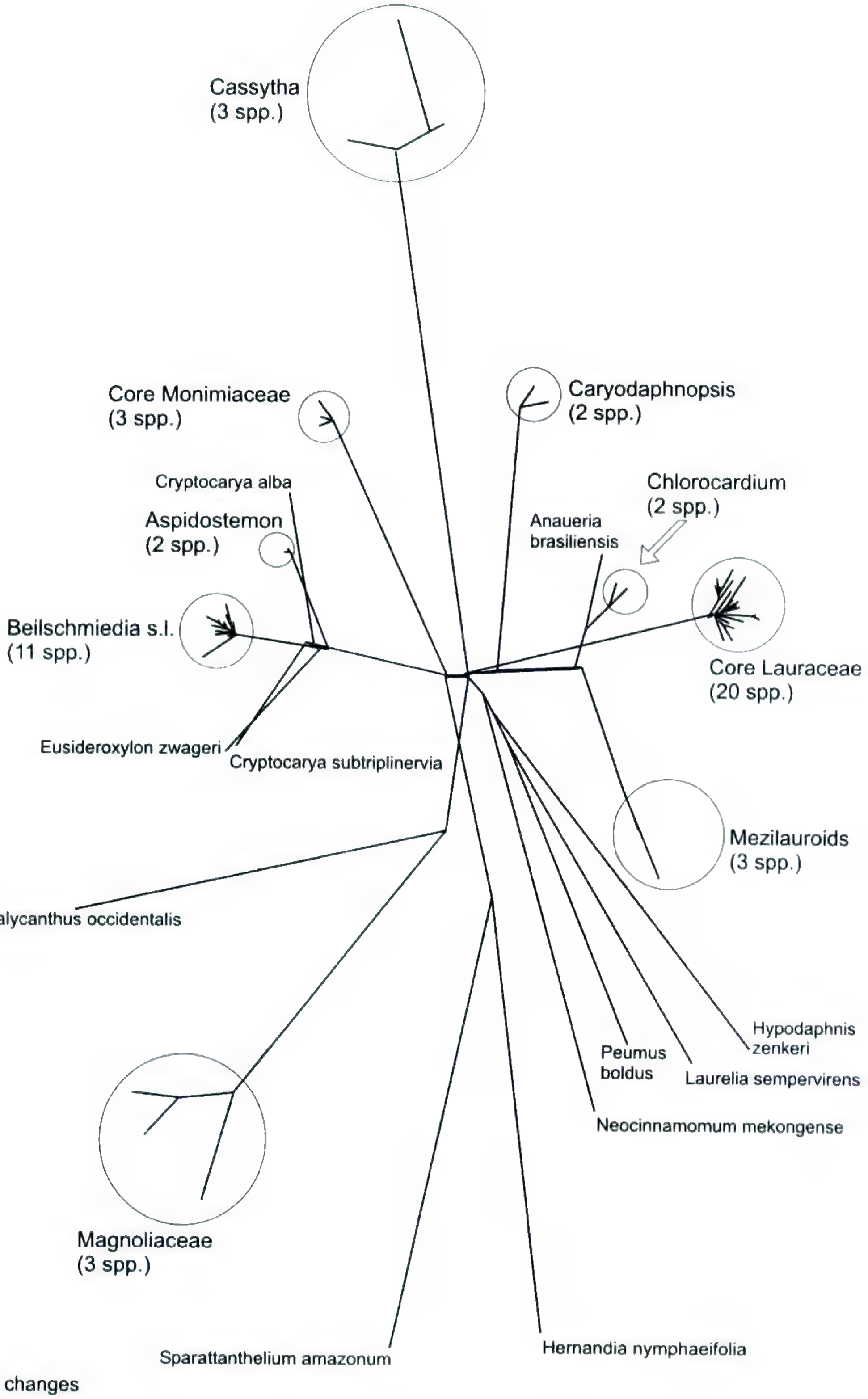

Figure 1. Unrooted distance tree (absolute number of differences, star decomposition search) obtained from the full large matrix with the star decomposition algorithm implemented in PAUP. Ellipses mark the nine groups that are replaced by their consensus sequences in the simplified matrices. The groups include the following species: *Aspidostemon* (*A. parvifolium*, *Aspidostemon* sp. indet.); *Beilschmiedia* s.l. (*B. berteroana*, *B. brenesii*, *B. madagascariensis*, *B. mexicana*, *B. miersii*, *B. roxburghiana*, *B. tawa*, *Endiandra impressicosta*, *E. kingiana*, *E. pubens*, *Potameia chartacea*);

analysis could become compatible with more than one of these topologies when taxa were excluded or when branches collapsed. In the absence of *Neocinnamomum*, e.g., there is no difference between the topologies 1 and 2.

In the following, we describe in detail only the results of the two most comprehensive analyses (complete large matrix, parsimony, and Bayesian), which also represent the two most frequently retrieved topologies. In all other cases, we will mention only the most important differences. The tree scores for the parsimony analyses are given in Table 5.

Analyses 1 and 2, complete large matrix

The result of Analysis 1 (complete large matrix, parsimony) corresponds to topology 1 in Figure 2. The full bootstrap, fast bootstrap, and jackknife trees are very similar to one another and free from conflicts, mostly with a slightly better resolution in the full bootstrap. The combinable component consensus of these three analyses (not shown, but very similar to Fig. 3) shows a strongly supported (100% in all three measures of support) but poorly resolved Perseeae–Laureae clade (henceforth called "Core Lauraceae") as sister to a weakly to moderately supported clade (67% bootstrap = BS/70% fast bootstrap = FBS/68% jackknife = JK) comprising *Anaueria*, *Chlorocardium*, *Mezilaurus*, *Sextonia*, and *Williamodendron* (henceforth called "Mezilaurus group"). Two subclades within this Mezilaurus group, one with the two species of *Chlorocardium* and the other with *Mezilaurus*, *Sextonia*, and *Williamodendron* (these three henceforth called "Mezilauroids") receive 99% (*Chlorocardium*, BS and FBS) or 100% support. Within the Mezilauroids, *Sextonia* and *Williamodendron* form a weakly to moderately supported clade (78 BS/72 FBS/59 JK). All of the above clades form a strongly (invariably 100%) supported group, for which a sister-group relationship with *Caryodaphnopsis* receives weak to moderate support (78/54/71). *Cassytha* and *Neocinnamomum* form a clade that is moderately supported in the full bootstrap and jackknife analyses (84% and 80%, respectively), but only weakly supported (67%) in the fast bootstrap. In the full bootstrap and the jackknife analyses, this group is strongly supported (91% and 90%, respectively) as sister group to all of the taxa mentioned above, whereas this grouping receives only weak support (53%) in the fast bootstrap. Sister to all of the above taxa is a very strongly (invariably 100%) supported clade comprising *Aspidostemon*, *Beilschmiedia*, *Cryptocarya*, *Endiandra*, *Eusideroxylon*, and *Potameia*. Within this clade (henceforth called "Cryptocarya group"), there is invariably 100% support for *Aspidostemon* and for *Beilschmiedia* s.l., including *Endiandra* and *Potameia*, as well as strong support (100/91/100) for a sister-group relationship of these taxa with *Cryptocarya*. The two species of *Cryptocarya* (99/94/98) as well as *Endiandra impressicosta* and *E. kingiana* (96/95/81) also form strongly supported clades. Other groupings within the Cryptocarya group receive only weak to moderate support (all taxa except *Aspidostemon* 72/66/66; *Beilschmiedia berteroana* and *B. miersii* 65/61/56; all remaining species 63/-/51; *B. brenesii* and *B. mexicana* 80/86/77; *B. madagascariensis* and *Potameia chartacea* 60/64/51; *B. tawa* and the three species of *Endiandra* 79/74/62; *Endiandra* 51/-/-). Finally, the Lauraceae except *Hypodaphnis* are moderately (71% FBS) to strongly (92% BS, 90% JK) supported as a monophyletic group, whereas the inclusion of *Hypodaphnis* in the Lauraceae receives only weak (55% JK) or no support. The Lauraceae form a strongly supported (98/92/95) but unresolved group with the Hernandiaceae (invariably 100% support) and the Monimiaceae (100/95/99). Within the Monimiaceae, a core group consisting of *Hedycarya arborea*, *Tambourissa religiosa*, and *Wilkiea huegeliana* (henceforth called "Core Monimiaceae") invariably received 100% support. Between the Lauraceae–Hernandiaceae–Monimiaceae clade and the outgroup Magnoliaceae there is a well-supported grade of *Laurelia sempervirens* (Atherospermataceae) and *Calycanthus occidentalis* (Calycanthaceae), the latter being sister to all other Laurales. This grade was invariably retrieved from all analyses, and therefore it will not be mentioned any more below.

←

Caryodaphnopsis (*C. bilocellata*, *C. tomentosa*); *Cassytha* (*C. ciliolata*, *C. melantha*, *C. pubescens*); *Chlorocardium* (*C. rodiei*, *C. venenosum*); Core Lauraceae (*Actinodaphne borneensis*, *A. diversifolia*, *Alseodaphne perakensis*, *Aniba affinis*, *Apollonias barbujana*, *Cinnamomum camphora*, *Dehaasia cuneata*, *Endlicheria verticillata*, *Laurus azorica*, *Licaria triandra*, *Lindera benzoin*, *Nectandra coriacea*, *Ocotea foetens*, *O. malcomberi*, *O. paulii*, *Persea americana*, *P. grijsii*, *P. indica*, *Sassafras tzumu*, *Umbellularia californica*); Core Monimiaceae (*Hedycarya arborea*, *Tambourissa religiosa*, *Wilkiea huegeliana*); Mezilauroids (*Mezilaurus opaca*, *Sextonia rubra*, *Williamodendron glaucophyllum*); Magnoliaceae (*Liriodendron tulipifera*, *Magnolia macrophylla*, *Michelia figo*).

Table 3. Model parameters suggested by ModelTest 3.06 according to the hierarchical Likelihood Ratio Test.

Partition	Model selected	Base frequencies				Rate matrix						Gamma shape parameter
		A	C	G	T	A–C	A–G	A–T	C–G	C–T	G–T	
Coding, full matrix	TVM+G	0.2959	0.1778	0.1618	0.3645	1.3562	2.7175	0.1775	0.8444	2.7175	1.0000	0.9005
Non-coding, full matrix	GTR+G	0.3338	0.1528	0.2060	0.3075	0.9352	1.7801	0.2627	0.6860	2.9092	1.0000	0.8706
Coding simplified	TVM+G	0.2970	0.1800	0.1611	0.3619	1.5927	3.3094	0.2218	1.0413	3.3094	1.0000	0.8521
Non-coding simplified	GTR+G	0.3343	0.1550	0.2017	0.3089	0.9536	1.8534	0.2827	0.7357	2.9661	1.0000	0.7611

The result of Analysis 2 (complete large matrix, Bayesian; Fig. 3) corresponds to topology 2 in Figure 2. It is somewhat more resolved than the consensus trees of the parsimony analyses, especially within the Core Lauraceae, which are resolved into a strongly supported Persea clade as sister to a moderately supported clade including taxa traditionally referred to the Laureae and the Cinnamomeae. The traditional Laureae are found largely unresolved at the base, whereas the Cinnamomeae form a strongly supported clade. *Sassafras tzumu* is weakly supported as sister group to the Cinnamomeae. Within the Cinnamomeae, the two Old World species of *Ocotea* and all Neotropical taxa except *Nectandra coriacea* (but including *Ocotea paulii*) form two strongly supported clades. Within the latter, *Aniba affinis*, *Endlicheria verticillata*, and *Ocotea paulii* form a clade with considerable support. Most other clades retrieved from the Bayesian analysis are congruent with the results of the parsimony analyses, with two exceptions: the Hernandiaceae and the Monimiaceae, which formed an unresolved trichotomy with the Lauraceae in the parsimony analyses, now form a weakly supported clade, and *Neocinnamomum* has moved from a moderately supported position as sister to *Cassytha* to a weakly supported position as sister to *Caryodaphnopsis*. This is the only conflicting result obtained with the two methods of analysis.

As a result of these analyses, we simplified the matrix by creating consensus sequences as described above from (1) all taxa of the Core Lauraceae, (2) the three Mezilauroid genera *Mezilaurus*, *Sextonia*, and *Williamodendron*, (3) the two species of *Chlorocardium*, (4) the two species of *Caryodaphnopsis*, (5) the three species of *Cassytha*, (6) the two species of *Aspidostemon*, (7) all species of *Beilschmiedia* s.l., including *Endiandra* and *Potameia*, (8) the three Core Monimiaceae *Hedycarya*, *Tambourissa*, and *Wilkiea*, and (9) the three Magnoliaceae.

Analyses 3–13, complete simplified matrix

Analysis 3 is a duplication of Analysis 1 (complete matrix, parsimony) with the simplified (20 taxa) matrix. As expected, it shows the same topology, with a slight increase in most bootstrap values. Among the taxon deletion experiments (Analyses 4 through 9), only deletion of *Cassytha* (Analysis 4) and deletion of both *Cassytha* and *Hypodaphnis* (Analysis 7) lead to a change in topology within the Lauraceae compared to Analysis 1, namely the placement of *Caryodaphnopsis* and *Neocinnamomum* in a common clade in the strict con-

sensus (topology 2 in Fig. 2), albeit without bootstrap support in Analysis 4. However, the Hernandiaceae plus Monimiaceae clade collapses in Analyses 4 (excl. *Cassytha*), 6 (excl. *Neocinnamomum*), and 8 (excl. *Cassytha* and *Neocinnamomum*).

Analysis 10 is a duplication of Analysis 2 (complete matrix, Bayesian) with the simplified matrix. As expected, it shows no change except a slight increase in some posterior probabilities. This increase also leads to weak support for a sister-group relationship between *Chlorocardium* and the Mezilauroids, whereas the relationship among the three main taxa of the Mezilaurus group (*Anaueria*, *Chlorocardium*, and the Mezilauroids) was unresolved in all previous analyses. Two of the three taxon deletion experiments (Analysis 11, excl. *Cassytha*, and 13, excl. *Neocinnamomum*) changed the topology within this group to weak support for a sister-group relationship between *Anaueria* and the Mezilauroids, but otherwise had no effect.

Analyses 14 and 15, coding large matrix

The result of Analysis 14 (coding large matrix, parsimony) is compatible with that of Analysis 1, but less resolved. In general, strongly supported clades from the complete large matrix retain their strong support, moderate support values often decrease, and weakly supported clades tend to disappear. Notable are the following changes: (1) the clade including *Aniba affinis*, *Endlicheria verticillata*, *Licaria triandra*, *Ocotea paulii*, and *Umbellularia californica* is no longer present, (2) a weakly supported Persea group (61% FBS) including *Alseodaphne perakensis*, *Apollonias barbujana*, *Dehaasia cuneata*, and the three species of *Persea*, appears within the Core Lauraceae, (3) support for the clade including all genera of the Cryptocarya group except *Aspidostemon* increases (83% vs. 66% FBS), (4) support for the Lauraceae except *Hypodaphnis* decreases strongly (55% vs. 71% FBS), (5) support for the Lauraceae including *Hypodaphnis* increases dramatically (87% vs. no support in the FBS). The result of Analysis 15 (coding large matrix, Bayesian) is likewise compatible with its counterpart from the complete large matrix (Analysis 2), but less resolved. The only new feature is weak support for a sister-group relationship of *Anaueria* to the Mezilauroids.

A maximum likelihood analysis of the coding large matrix (not included in Table 4) took 10 days to complete and yielded almost the same topology as the Bayesian analysis, with two notable exceptions: the *Persea* group became sister to the Laureae–Cinnamomeae, and *Anaueria* instead of *Chlorocardium* became sister to the rest of the Mezilaurus group.

Analyses 16–30, coding simplified matrix

Simplification of the coding matrix (Analyses 16 = parsimony and 23 = Bayesian) caused almost no significant change, not even a consistent change in the support values. It should be noted, however, that in the latter analysis (23) there was a change in the Mezilaurus group toward weak support for a sister-group relationship of *Chlorocardium* to the Mezilauroids.

In the parsimony analyses, most of the taxon deletion experiments performed on the coding simplified matrix yielded similar results to those performed on the complete simplified matrix. Deletion of *Cassytha* (Analysis 17) and deletion of both *Cassytha* and *Hypodaphnis* (Analysis 20) again led to the placement of *Caryodaphnopsis* and *Neocinnamomum* in a weakly supported common clade (topology 2 in Fig. 2), and the Hernandiaceae plus Monimiaceae clade collapsed in Analyses 17 (excl. *Cassytha*) and 21 (excl. *Cassytha* and *Neocinnamomum*). However, deletion of *Neocinnamomum* alone (Analysis 19) led to a most notable change in topology (topology 3 in Fig. 2); *Cassytha* moved to a weakly supported position as sister group to *Hypodaphnis*. When both *Neocinnamomum* and *Hypodaphnis* were excluded (Analysis 22), *Cassytha* retained its original position below *Caryodaphnopsis*.

Deletion of taxa had no effect on the results of the Bayesian analyses (Analysis 24 through 26), except that deletion of *Cassytha* (Analysis 24) or *Neocinnamomum* (Analysis 26) restored weak support for a sister-group relationship of *Anaueria* to the Mezilauroids, as in the large matrix (Analysis 15).

The results of the maximum likelihood analyses of the coding simplified matrix (Analyses 27 through 30) are fully congruent with the results of the Bayesian analyses, including the changes in topology within the Mezilaurus group.

Analyses 31–47, non-coding matrices

The results of the analyses of the non-coding part of the matrix (topologies 4 and 5 in Fig. 2) consistently differ from those of the complete or coding matrices in three notable characteristics. First, the Mezilaurus group is never supported as a clade. Instead, its three main taxa (*Anaueria*, *Chlorocardium*, and the Mezilauroids) form a polytomy, in which the Core Lauraceae constitute the fourth branch. Second, within the Cryptocarya group, *Eu-*

Table 4. Support values of branches I–X in the different phylogenetic analyses (see Fig. 2 for clade numbers). Top = no. of compatible topology in Figure 2. Roman clade numbers as in Figure 2: I = Mezilaurus group, II = Core Lauraceae + Mezilaurus group + *Caryodaphnopsis* (in topology 2 and 4 also including *Neocinnamomum*), III = *Cassytha* + *Neocinnamomum*, IV = *Caryodaphnopsis* + *Neocinnamomum*, V = above the Cryptocarya group, VI = below the Cryptocarya group, VII = monophyletic Lauraceae, VIII = Hernandiaceae + Monimiaceae, IX = Monimiaceae incl. *Peumus*, X = Hernandiaceae + *Hypodaphnis*. Symbols in the table: + = clade present in the majority consensus, but support < 50%; p = members of clade collapsed into a polytomy; – = clade incompatible with this analysis; -p- = clade incompatible with the majority consensus but collapsed in the bootstrap consensus; n.a. = not applicable (due to exclusion of one of the taxa); ! = clade present, but no bootstrap analysis performed because of long calculation times.

No.	Matrix	Analysis	Top.	I	II	III	IV	V	VI	VII	VIII	IX	X
1.	complete large (60 taxa[1])	parsimony	1	67–70	54–78	67–84	–	53–92	71–92	#55	p	95–100	–
2.	complete large	Bayesian	2	82	99	–	53	100	100	100	69	100	–
3.	complete simplified (20 taxa[2])	parsimony	1	77	74	91	–	96	96	51	p	99	–
4.	excl. *Cassytha*	parsimony	1, 2	75	93	n.a.	+	= II	93	52	p	98	–
5.	excl. *Hypodaphnis*	parsimony	1	79	75	90	–	98	100	= VI	64	93	n.a.
6.	excl. *Neocinnamomum*	parsimony	1, 2	73	80	n.a.	n.a.	84	90	60	p	100	–
7.	excl. *Cassytha & Hypodaph.*	parsimony	2	88	97	n.a.	56	= II	99	= VI	66	94	n.a.
8.	excl. *Cassytha & Neocinn.*	parsimony	1, 2	54	100	n.a.	n.a.	= II	100	57	p	100	–
9.	excl. *Hypodaph. & Neocinn.*	parsimony	1, 2	78	75	n.a.	n.a.	73	98	= VI	56	92	n.a.
10.	complete simplified	Bayesian	2	86[c]	97	–	55	100	100	100	80	99	–
11.	excl. *Cassytha*	Bayesian	2	77[d]	100	n.a.	53	= II	100	99	81	100	–
12.	excl. *Hypodaphnis*	Bayesian	2	91[c]	99	–	62	100	100	= VI	57	100	n.a.
13.	excl. *Neocinnamomum*	Bayesian	1, 2	62[d]	99	n.a.	n.a.	100	100	100	74	99	–
14.	coding large (64 taxa[3])	parsimony	1	73	57	76	–	68	55	87	+	98	–
15.	coding large	Bayesian	2	90[c]	98	–	84	88	74	100	81	100	–
16.	coding simplified (21 taxa[4])	parsimony	1	77	62	78	–	73	54	84	54	99	–
17.	excl. *Cassytha*	parsimony	2	63	85	n.a.	56	= II	59	77	p	98	–
18.	excl. *Hypodaphnis*	parsimony	1	79	74	94	–	86	94	= VI	61	96	n.a.
19.	excl. *Neocinnamonum*	parsimony	3	57	79	n.a.	n.a.	= II	+	90	52	98	–
20.	excl. *Cassytha & Hypodaph.*	parsimony	2	81	87	n.a.	64	= II	89	= VI	62	96	n.a.
21.	excl. *Cassytha & Neocinn.*	parsimony	1, 2	59	100	n.a.	n.a.	= II	73	90	p	98	–
22.	excl. *Hypodaph. & Neocinn.*	parsimony	1, 2	70	62	n.a.	n.a.	52	81	= VI	56	97	n.a.
23.	coding simplified	Bayesian	2	93[c]	94	–	82	99	82	100	78	100	–
24.	excl. *Cassytha*	Bayesian	2	81[d]	100	n.a.	83	= II	80	100	81	100	–
25.	excl. *Hypodaphnis*	Bayesian	2	97[c]	98	–	82	95	100	= VI	84	99	n.a.
26.	excl. *Neocinnamomum*	Bayesian	1, 2	83[d]	98	n.a.	n.a.	78	72	100	78	100	–
27.	coding simplified	likelihood	2	60[(c)]	72	–	52	77	59	93	64	91	–
28.	excl. *Cassytha*	likelihood	2	![d]	!	n.a.	!	= II	!	!	!	!	–
29.	excl. *Hypodaphnis*	likelihood	2	![c]	!	–	!	!	!	= VI	!	!	n.a.
30.	excl. *Neocinnamomum*	likelihood	1, 2	![d]	!	n.a.	n.a.	!	!	!	!	!	–

Table 4. Continued.

No.	Matrix	Analysis	Top.	I	II	III	IV	V	VI	VII	VIII	IX	X
31.	non-coding large (59 taxa[5])	parsimony	4	p	+	-p-	-p-	55	69	–	+	+	50
32.	non-coding large	Bayesian	5	p	p	–	p	100	100	–	–	–	88
33.	non-coding simplified (20 taxa[2])	parsimony	4[a]	p	–	–	–	81	90	–	+	51	67
34.	excl. *Cassytha*	parismony	4[b]	p	51	n.a.	–	77	90	–	+	56	58
35.	excl. *Hypodaphnis*	parsimony	4[a]	p	–	–	–	71	94	= VI	p	53	n.a.
36.	excl. *Neocinnamomum*	parsimony	4	p	74	n.a.	n.a.	91	97	–	+	51	68
37.	excl. *Cassytha & Hypodaph.*	parsimony	4	p	88	n.a.	-p-	= II	97	= VI	p	p	n.a.
38.	excl. *Cassytha & Neocinn.*	parsimony	4	p	98	n.a.	n.a.	= II	99	–	+	52	66
39.	excl. *Hypodaph. & Neocinn.*	parsimony	1, 2, 4	p	67	n.a.	n.a.	86	98	= VI	p	54	n.a.
40.	non-coding simplified	Bayesian	5	p	61	–	p	98	100	–	–	–	80
41.	excl. *Cassytha*	Bayesian	5	p	100	n.a.	p	= II	100	–	–	–	89
42.	excl. *Hypodaphnis*	Bayesian	5	p	60	–	p	100	99	–	p[c]	–	n.a.
43.	excl. *Neocinnamomum*	Bayesian	5	p	74	n.a.	n.a.	99	100	–	–	–	85
44.	non-coding simplified	likelihood	5	p	100	-p-	-p-	85	96	-p-	-p-	-p-	+
45.	excl. *Cassytha*	likelihood	5	p	!	n.a.	–	!	!	–	–	–	!
46.	excl. *Hypodaphnis*	likelihood	5	p	!	–	–	!	!	–	–	–	n.a.
47.	excl. *Neocinnamomum*	likelihood	5	p	!	n.a.	n.a.	!	!	–	–	–	!

[1] Excluding *Dodecadenia grandiflora*, *Gyrocarpus americanus*, *Iteadaphne caudata*, and *Parasassafras confertiflora*, because only a partial coding sequence of these taxa was retrieved from EMBL.

[2] Including the taxa and species groups shown in Figure 1.

[3] Including all taxa.

[4] Including the taxa and species groups shown in Figure 1, plus the sequence of *Gyrocarpus americanus* retrieved from EMBL.

[5] Excluding *Dodecadenia grandiflora*, *Gyrocarpus americanus*, *Iteadaphne caudata*, and *Parasassafras confertiflora* (see above); sequences of *Beilschmiedia berteroana* and *B. miersii* identical in the non-coding region, therefore one sequence representing both species.

[a] Non fully compatible with the majority consensus, but with the bootstrap consensus.

[b] Not fully compatible with the bootstrap consensus, but with the majority consensus.

[c] Resolved as (*Anaueria* (*Chlorocardium* + Mezilauroids)).

[(c)] As previous, but collapsed in the bootstrap consensus.

[d] Resolved as (*Chlorocardium* (*Anaueria* + Mezilauroids)).

[e] Monimiaceae excluding *Peumus*.

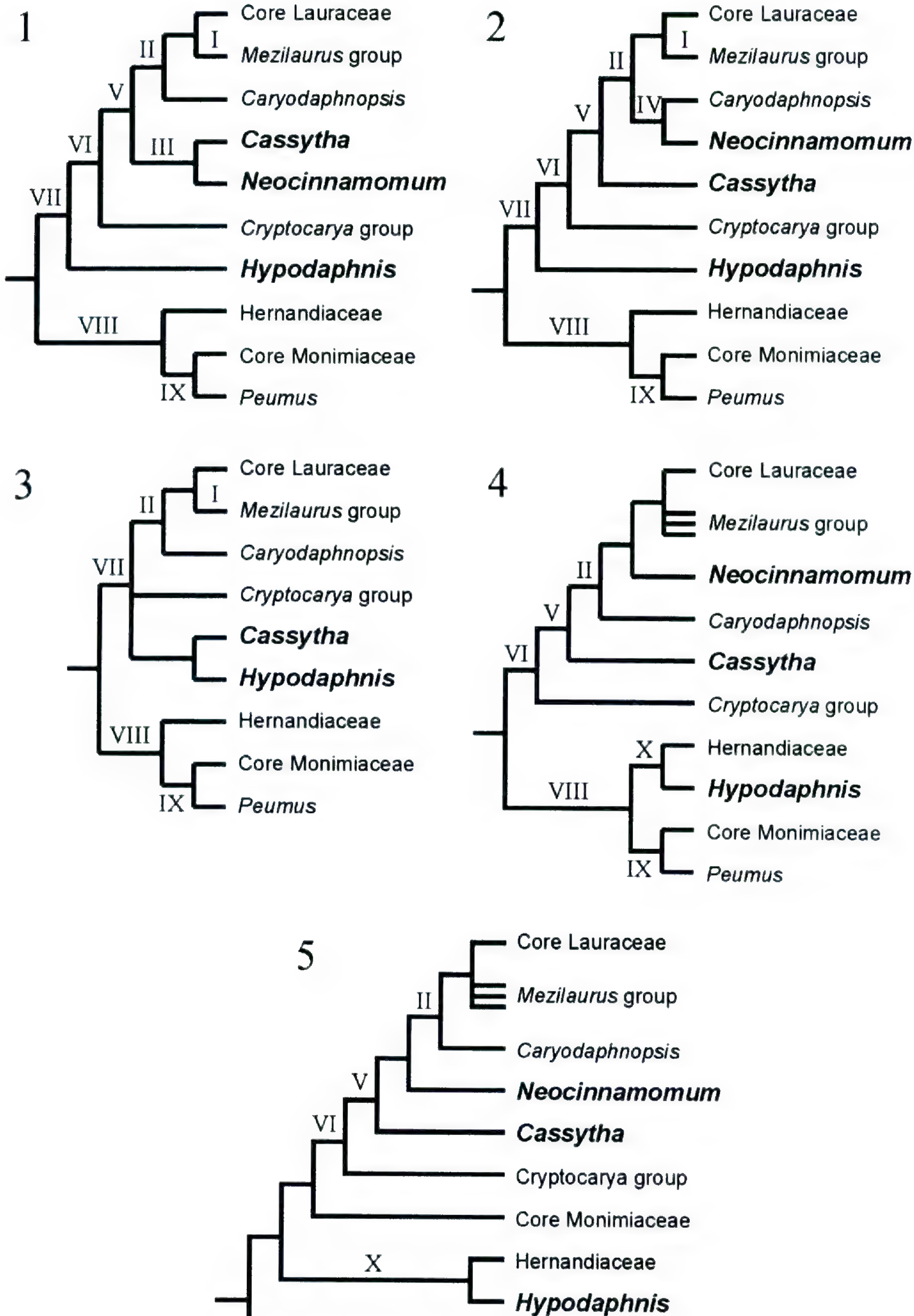

Figure 2. The five conflicting topologies retrieved from the 47 analyses of the data set. Names of genera with unstable positions in boldface. Roman numerals mark clades with variable support (see Table 4 for support values): I = Mezilaurus group; II = Core Lauraceae + Mezilaurus group + *Caryodaphnopsis* (in topology 2 and 4 also including *Neocinnamomum*); III = *Cassytha* + *Neocinnamomum*; IV = *Caryodaphnopsis* + *Neocinnamomum*; V = above the Cryptocarya group; VI = below the Cryptocarya group; VII = monophyletic Lauraceae; VIII = Hernandiaceae + Monimiaceae; IX = Monimiaceae incl. *Peumus*; X = Hernandiaceae + *Hypodaphnis*. Support for the Core Lauraceae

Table 5. Tree scores of the parsimony analyses (numbers and included taxa as in Table 4). Uninf. = variable but parsimony-uninformative; inform. = parsimony-informative; CI = consistency index; RI = retention index.

		Characters			Results				
No.	Analysis matrix	Constant	Uninf.	Inform.	Trees	Length	Islands	CI	RI
1	complete large (60 taxa)	1411	398	623	3150	1802	1	0.708	0.864
3	complete simplified (20 taxa)	1519	554	362	15	1500	1	0.745	0.577
4	excl. *Cassytha*	1564	542	329	12	1351	1	0.765	0.613
5	excl. *Hypodaphnis*	1557	533	345	3	1394	1	0.765	0.608
6	excl. *Neocinnamomum*	1570	531	334	6	1385	1	0.757	0.599
7	excl. *Cassytha* & *Hypodaphnis*	1608	516	311	3	1245	1	0.786	0.648
8	excl. *Cassytha* & *Neocinnamomum*	1620	511	304	4	1226	1	0.783	0.649
9	excl. *Hypodaphnis* & *Neocinnamomum*	1609	511	315	3	1280	1	0.779	0.633
14	coding large (64 taxa)	867	237	414	15,435	1163	1	0.696	0.861
16	coding simplified (21 taxa)	930	348	240	6	965	1	0.739	0.581
17	excl. *Cassytha*	957	341	220	6	873	1	0.761	0.616
18	excl. *Hypodaphnis*	949	337	232	3	909	1	0.755	0.606
19	excl. *Neocinnamomum*	964	334	220	2	887	1	0.755	0.605
20	excl. *Cassytha* & *Hypodaphnis*	981	326	211	3	817	1	0.777	0.644
21	excl. *Cassytha* & *Neocinnamomum*	995	321	202	4	788	1	0.782	0.655
22	excl. *Hypodaphnis* & *Neocinnamomum*	983	325	210	8	835	1	0.770	0.628
31	non-coding large (59 taxa)	530	163	221	303	668	53	0.723	0.873
33	non-coding simplified (20 taxa)	580	202	135	9	549	1*	0.758	0.619
34	excl. *Cassytha*	598	196	123	5	492	1*	0.776	0.657
35	excl. *Hypodaphnis*	599	191	127	36	503	1	0.779	0.648
36	excl. *Neocinnamomum*	597	193	127	3	510	1*	0.767	0.642
37	excl. *Cassytha* & *Hypodaphnis*	618	184	115	20	446	1	0.798	0.689
38	excl. *Cassytha* & *Neocinnamomum*	616	185	116	2	453	1*	0.786	0.682
39	excl. *Hypodaphnis* & *Neocinnamomum*	617	181	119	12	464	1*	0.789	0.672

* Some of the addition sequence replicates ended on a different island (two additional islands in Analysis 36, three in Analysis 38) with trees one step longer than the most parsimonious trees.

sideroxylon is placed as sister to *Aspidostemon*, not to *Beilschmiedia* s.l. plus *Cryptocarya*, as in all other analyses. This relationship, however, receives no support in the maximum likelihood analysis and usually only weak support in the other analyses (up to 73% posterior probability in Analysis 46). Third, *Hypodaphnis* is invariably placed as sister to the Hernandiaceae instead of the Lauraceae, so that the Cryptocarya group forms the most basal branch within the Lauraceae.

In a parsimony analysis of the non-coding large matrix (Analysis 31, topology 4 in Fig. 2), the Core Lauraceae are largely unresolved, except for the weakly supported Cinnamomeae (compare Analysis 2, Fig. 3), which include a moderately supported clade comprising *Aniba affinis*, *Endlicheria verticillata*, *Licaria triandra*, *Ocotea paulii*, and *Umbellularia californica* (called "Aniba group" below). Below the Core Lauraceae plus Mezilaurus group, the strict consensus shows a grade of *Neocinnamomum*, *Caryodaphnopsis*, and *Cassytha* (in descending order). In the bootstrap consensus, this grade collapses into a polytomy. In a similar way, *Peumus* is sister to the Core Monimiaceae, and together they constitute the sister group to the Hernandiaceae plus Hypodaphnis clade in the strict consensus, whereas these taxa (*Peumus*, the Core Monimiaceae and the Hernandiaceae + Hypodaphnis clade) form a polytomy with the Lauraceae in the bootstrap consensus.

The result of the Bayesian analysis of the non-coding large matrix (Analysis 32, topology 5 in Fig. 2) shares many features with the result of the parsimony analysis, but also differs in certain aspects.

←

+ Mezilaurus group and for the Cryptocarya group is usually 100%, rarely 99%. Support for the branch below *Neocinnamomum* in topologies 4 and 5 varies from (mostly) absent to just moderate (up to 73% posterior probability in Analysis 32). Support for the branches below the Core Monimiaceae and below the Hernandiaceae + *Hypodaphnis* clade in topology 5 varies from absent to (mostly) moderate (up to 85% and 86% PP in Analysis 32, respectively).

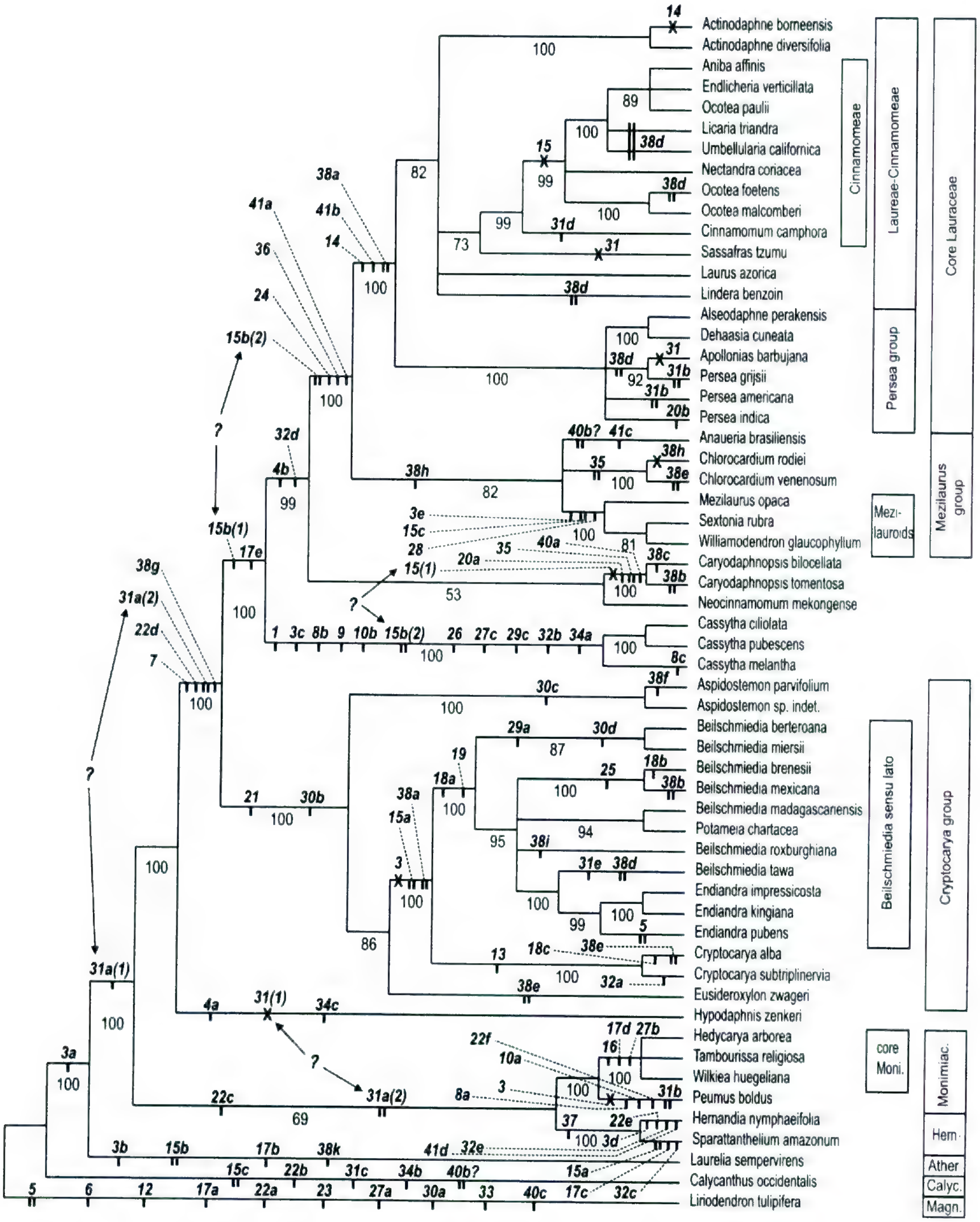

Figure 3. Result of Analysis 2 (see Table 4), Bayesian analysis of the complete large matrix. Numbers below branches are posterior probabilities, numbers in boldface/italics are numbers of potentially parsimony-informative indels in Table 6. | = singular character change, || = parallel character change, X = reversal. The characters 15 and 31 (marked with arrows) can be most parsimoniously mapped onto the cladogram in two different ways, (1) originating once and with two (#15) or three (#31) reversals, (2) originating twice in parallel and with one (#15) or two (#31) reversals. Ather. = Atherospermataceae; Calyc. = Calycanthaceae; Core Moni. = Core Monimiaceae; Hern. = Hernandiaceae; Monimiac. = Monimiaceae.

The Cinnamomeae, the Aniba group described above, and most of the other major clades are obtained with 100% posterior probability (PP). Even the sister-group relationship of *Hypodaphnis* to the Hernandiaceae receives considerable support (88%). The branch separating *Caryodaphnopsis* and *Neocinnamomum* is not supported, and the branch below *Neocinnamomum* receives only moderate (73%) support. In contrast to all previous analyses, the Core Monimiaceae appear as sister group to the Lauraceae, with 85% posterior probability. Sister to this group, with 86% PP, is the Hernandiaceae + Hypodaphnis clade, and *Peumus* appears to be sister to all of the above taxa (100%). Thus *Peumus* and the Core Monimiaceae are not sister groups in this topology, but separated by the Hernandiaceae between them.

Analysis 33 is a duplication of Analysis 31 (non-coding region, parsimony) with the simplified matrix, and as such it was expected to show the same topology (No. 4 in Fig. 2). In the majority consensus, however, *Caryodaphnopsis* and *Cassytha* swap places, but the branch between them receives only a slight majority (56%) and collapses in the bootstrap consensus. The common clade including the Hernandiaceae + *Hypodaphnis* and the Core Monimiaceae + *Peumus* also collapses in the bootstrap consensus.

Deletion of *Cassytha* (Analysis 34) does not change the topology of the majority rule consensus, but in the bootstrap consensus *Caryodaphnopsis* and *Neocinnamomum* swap places. The node separating them, however, receives only very weak (51%) support. Deletion of *Hypodaphnis* (Analysis 35) makes the Hernandiaceae, the Core Monimiaceae, and *Peumus* collapse into a polytomy in the majority consensus, whereas the sister-group relationship of the latter two taxa is maintained with weak support in the bootstrap consensus. Otherwise, there is no change compared to Analysis 33. Deletion of *Neocinnamomum* (Analysis 36) or of both *Cassytha* and *Neocinnamomum* (Analysis 38) retrieves topology 4 in Figure 2 unchanged (except for the deleted taxa) in the strict consensus, but without bootstrap support for the Hernandiaceae (+ *Hypodaphnis*) plus Monimiaceae (incl. *Peumus*) clade. Topology 5, however, is only one step longer.

Deletion of both *Cassytha* and *Hypodaphnis* (Analysis 37) makes the Hernandiaceae, the Core Monimiaceae, and *Peumus* collapse into a polytomy with the Lauraceae. Therefore, the only reason to prefer topology 4 over topologies 1, 2, or 5 (Fig. 2) is the fact that *Neocinnamomum* is placed above *Caryodaphnopsis* in 12 of the 20 most parsimonious trees. This branch, however, collapses in the strict and the bootstrap consensus. If both *Hypodaphnis* and *Neocinnamomum* are deleted (Analysis 39), the same outgroup clades as in Analysis 37 collapse into a polytomy with the Lauraceae in the majority rule consensus. However, the Core Monimiaceae + *Peumus* clade receives weak bootstrap support, so that the result is compatible with the topologies 1, 2, and 4 in Figure 2, but not with topology 3 or 5.

Analysis 40 is a duplication of Analysis 32 (non-coding region, Bayesian) with the simplified matrix, and it shows the same topology (No. 5 in Fig. 2). The branches above *Cassytha* and above *Peumus*, however, receive only weak support, and the branches linking the Core Monimiaceae to the Lauraceae and *Hypodaphnis* to the Hernandiaceae are only moderately supported. Deletion of *Cassytha*, *Hypodaphnis*, or *Neocinnamomum* (Analyses 41–43) does not significantly change the topology, except that the branch separating the Lauraceae + Core Monimiaceae from the Hernandiaceae collapses upon deletion of *Hypodaphnis*.

All maximum likelihood analyses of the non-coding simplified matrix (Analyses 44–47) retrieve topology 5 of Figure 2 in its fully resolved form, without any change in the taxon deletion experiments. In the bootstrap consensus, however, many branches collapse, so that the cladogram becomes compatible with any topology except No. 3 in Figure 2.

INDEL MAPPING

The complete large matrix contains a total of 38 parsimony-informative indels or regions of uncertain alignment, from which it was possible to extract 41 informative characters (Table 6; matrix available from the authors). Most of them are not homoplastic in any of the topologies in Figure 2. About half of the characters (22) simply characterize unequivocally monophyletic groups: five separate the Magnoliaceae from all other taxa (#6, 12, 23, 27, and 33 in Table 6), five *Cassytha* (#1, 9, 26, 27, and 34), three *Magnolia* + *Michelia* (#2, 11, and 39), two the Core Lauraceae + *Mezilaurus* group (#24 and 36), two *Beilschmiedia* s.l. (#18, with a secondary change in *B. brenesii*, and #19), two of the Core Monimiaceae (#16 and 27), and one each of the Hernandiaceae (#37), the Cryptocarya group (#21), the genus *Cryptocarya* (#13), *Beilschmiedia brenesii* + *B. mexicana* (#25), and the Mezilauroids (#28). Four additional indels (#20, 29, 30, and 41) are most easily explained as independent insertion/deletion events in the same region, in the latter two cases followed by point mutations in some taxa.

Indel #40 is non-homoplastic with respect to the

Table 6. Possibly informative characters derived from indels or regions of uncertain alignment.

Char. #	From pos.	To pos.	Most likely event, or sequence of indel	Taxa (and remarks)
1	147	152	duplication TAGAAT	*Cassytha*
2	158	164	7 bp deletion	*Magnolia, Michelia*
3	207	211	gap	Magnoliaceae, *Calycanthus, Peumus, Beilschmiedia* s.l. + *Cryptocarya*
3a			duplication TTCTT	most Laurales, incl. Lauraceae
3b			mutation TT**G**TT	*Laurelia*
3c			mutation TT**A**TT	*Cassytha*
3d			two mutations TT**A**T**C**	*Hernandia*
3e			mutation TTC**G**T	*Mezilaurus, Sextonia, Williamodendron* (= Mezilauroids)
4	240		C	all taxa except those below
4a			T	*Hypodaphnis* (but alignment uncertain)
4b			1 bp deletion	Core Lauraceae, Mezilaurus group, *Caryodaphnopsis, Neocinnamomum*
5	278		duplication A	Magnoliaceae, *Endiandra pubens*
6	324		duplication T	all Laurales incl. Lauraceae (or 1 bp deletion in Magnoliaceae)
7	330	333	duplication TGTT	all Lauraceae except *Hypodaphnis*
8	348	352	gap	all taxa except those below
8a			duplication ATTCG	*Peumus*
8b			mutation/insertion **G**TTCG	*Cassytha ciliolata* and *C. pubescens*
8c			mutation GTTC**A**	*Cassytha melantha*
9	432		1 bp deletion (G in all others)	*Cassytha*
10	455	461	insertion/deletion of T's	(poly-T region with 6 to 13 T's, precise number often uncertain)
10a			CCCCCTTTTT	*Peumus*
10b			TC	*Cassytha*
11	477	483	duplication TAACTAT	*Magnolia* + *Michelia*
12	490	493	duplication TTCT	Magnoliaceae
13	498	514	5 bp deletion	*Cryptocarya*
14	501	512	duplication TTCTCTAT-TATG	Core Lauraceae except *Actinodaphne borneensis*
15	583		A	all taxa except those below (*Neocinnamomum* unknown)
15a			gap 1 bp larger	*Beilschmiedia* s.l. + *Cryptocarya, Sparattanthelium*
15b			C	*Actinodaphne, Cinnamomum, Sassafras, Laurus, Lindera,* Persea group, *Anaueria, Chlorocardium, Cassytha, Laurelia*
15c			T	Mezilauroids, *Calycanthus*
16	653	658	duplication CTCTTG	Core Monimiaceae
17	693	696	AAGA	*Calycanthus, Peumus, Hernandia, Hypodaphnis*, Cryptocarya group
17a			GAGA	Magnoliaceae
17b			AGA	*Laurelia*
17c			AAAAAA	*Sparattanthelium*
17d			ACGA	Core Monimiaceae
17e			Gap	most Lauraceae, except those above (*Neocinnamomum* unknown)
18	744	746	larger gap	all taxa except those below (*Neocinnamomum* unknown)
18a			duplication T	*Beilschmiedia* s.l.
18b			mutation to G	*Beilschmiedia brenesii*
18c			duplication TTT	*Cryptocarya alba*
19	757		duplication A	*Beilschmiedia* s.l.
20	762		larger gap	all taxa except those below (*Neocinnamomum* unknown)
20a			duplication A	*Caryodaphnopsis*
20b			insertion C	*Persea indica*
21	772	776	duplication ATACC	Cryptocarya group

Table 6. Continued.

Char. #	From pos.	To pos.	Most likely event, or sequence of indel	Taxa (and remarks)
22	832	839	GTTT	*Hypodaphnis, Laurelia*
22a			GCCTTT	Magnoliaceae
22b			GCTTTTGT	*Calycanthus*
22c			GCTT	Core Monimiaceae, *Sparattanthelium*
22d			gap	Lauraceae except *Hypodaphnis* (*Neocinnamomum* unknown)
22e			ACTT	*Hernandia*
22f			GCCTT	*Peumus*
23	840	848	9 bp deletion	Magnoliaceae
24	861	866	duplication AATGGA	Core Lauraceae + Mezilaurus group (*Neocinnamomum* unknown)
25	911	916	6 bp deletion	*Beilschmiedia brenesii* + *B. mexicana*
26	2449	2453	5 bp deletion	*Cassytha*
27	2465		C	all taxa, except those below
27a			A	Magnoliaceae
27b			gap	Core Monimiaceae
27c			T	*Cassytha*
28	2482	2486	duplication ATGAA	Mezilauroids
29	2499	2502	larger gap	all taxa except those below
29a			duplication CA	*Beilschmiedia berteroana* + *B. miersii*
29b			insertion AGAA	*Magnolia* + *Michelia*
29c			high, variable no. of A's	*Cassytha*
30	2508	2513	larger gap	all taxa except those below
30a			insertion CCAA	Magnoliaceae (or deletion in Laurales)
30b			duplication CAAAA	*Cryptocarya* group (except for taxa mentioned below, and larger gap in *Eusideroxylon*, in a position different from that in the other taxa)
30c			1st CAAAA → TAAAA	*Aspidostemon*
30d			2nd CAAAA → TAAAA	*Beilschmiedia beteroana* + *B. miersii*
			uncertain, gap size different	*Calycanthus, Cassytha, Eusideroxylon*
31	2514	2516	AAA	*Apollonias, Sassafras, Hypodaphnis, Laurelia*, Magnoliaceae
31a			GAA	most taxa, except those above and below
31b			TAA	*Persea americana, Persea grijsii, Peumus*
31c			AAT	*Calycanthus*
31d			TCA	*Cinnamomum camphora*
31e			CAA	*Beilschmiedia tawa*
			uncertain, gap size different	*Cassytha, Cryptocarya subtriplinervia, Eusideroxylon*
32	2569	2573	duplication TAGTG	Magnoliaceae, *Calycanthus, Laurelia*, Monimiaceae incl. *Peumus, Hypodaphnis*, Cryptocarya group
32a			mutation TAGT**A**	*Cryptocarya subtriplinervia*
32b			mutation T**G**GTG	*Cassytha*
32c			two mutations T**GG**T**T**	*Sparattanthelium*
32d			gap (5 bp deletion)	Core Lauraceae, Mezilaurus group, *Caryodaphnopsis, Neocinnamomum*
32e			6 bp deletion in different pos.	*Hernandia*
33	2584	2588	5 bp deletion	Magnoliaceae
34	2620		C	all other taxa except those below (*Sextonia* unknown)
34a			A	*Cassytha*
34b			9 bp deletion (2619–2627 ?)	*Calycanthus*
34c			10 bp deletion (2618–2627 ?)	*Hypodaphnis*
35	2621		C	*Caryodaphnopsis, Chlorocardium*
			T	all other taxa (except *Calycanthus* and *Hypodaphnis*, see char. #34; *Sextonia* unknown)

Table 6. Continued.

Char. #	From pos.	To pos.	Most likely event, or sequence of indel	Taxa (and remarks)
36	2623		T	Core Lauraceae + Mezilaurus group
			C	all other taxa (except *Calycanthus* and *Hypodaphnis*, see char. #34; *Sextonia* unknown)
37	2625		G	Hernandiaceae
			A	all other taxa (except *Calycanthus* and *Hypodaphnis*, see char. #34; *Sextonia* unknown)
38	2701	2705	insertion/deletion of T's or G's	(poly-T + poly-G region, T's and G's counted in central region of uncertain alignment only)
			0 T's/3 G's	Magnoliaceae, all Laurales except Lauraceae but incl. *Hypodaphnis*
38a			4 T's/0 G's	most Lauraceae, except *Hypodaphnis* and the taxa mentioned below
38b			4 T's/1 G	*Beilschmiedia mexicana, Caryodaphnopsis tomentosa*
38c			3 T's/2 G's	*Caryodaphnopsis bilocellata*
38d			3 T's/1 G	*Apollonias, Beilschmiedia tawa, Licaria, Lindera, Ocotea foetens, Persea grijsii, Umbellularia*
38e			3 T's/0 G's	*Chlorocardium venenosum, Cryptocarya alba, Eusideroxylon*
38f			2 T's/2 G's	*Aspidostemon parvifolium*
38g			2 T's/1 G	*Aspidostemon* sp. indet., *Cassytha, Chlorocardium rodiei, Neocinnamomum*
38h			2 T's/0 G's	*Anaueria, Mezilaurus, Williamodendron (Sextonia* unknown)
38i			TGTT	*Beilschmiedia roxburghiana*
38k			GAG	*Laurelia*
39	2720		duplication T	*Magnolia + Michelia*
40	2724	2729	TATAT	most taxa, except those mentioned below (*Neocinnamomum* and *Sextonia* unknown)
40a			TGATAG = insertion G	*Caryodaphnopsis*
40b			TATT = deletion A	*Anaueria, Calycanthus* (in both genera other small gaps in close vicinity, therefore alignment uncertain)
40c			gap covering entire region	Magnoliaceae
41	2734	2738	5 bp gap	most taxa, except those mentioned below
41a			duplication TCTAT	*Chlorocardium, Mezilaurus, Williamodendron (Neocinnamomum* and *Sextonia* unknown)
41b			mutation TATAT	Core Lauraceae
41c			4 bp gap	*Anaueria* (other small gaps close by, alignment uncertain)
41d			9 bp gap	*Hernandia*

deletion of 5 bases in all Magnoliaceae and the insertion of a single base (G) in all species of *Caryodaphnopsis*, but might appear homoplastic in the deletion of a single base in *Anaueria* and *Calycanthus*. However, both genera have other small gaps in the close vicinity, so that the alignment is not entirely certain. Another indel (#10) cannot be used with confidence for the entire data set because it is a poly-T region, in which it is impossible to ascertain the precise number of bases in the repetitive sequence. However, the three species of *Cassytha* differ from all other taxa in having the second T replaced by a C. From the alignment, character #8 may also appear homoplastic, as a duplication of a 5 bp motif in *Peumus*, with subsequent modification in *Cassytha*. However, the two genera are not close to each other in any of the topologies, so that the different sequences of the insertions may be taken as evidence of their independent origin.

Two indels (#5 and 14) are inevitably homoplastic when using the large matrices but disappear in the simplified matrices, as they involve single taxa deviating from the general pattern of their group. Seven characters (#3, 15, 22, 31, 32, 35, and 38) are homoplastic in all five topologies in Figure 2.

They show identical character states that cannot be interpreted as retained plesiomorphies in taxa that cannot be considered closely related under any circumstances. Nevertheless, three of them (#22, 32, and 38) show a greater or lesser degree of homoplasy depending on the topology. In character #22 it appears most likely that there was a deletion within the Lauraceae after the separation of *Hypodaphnis* from the rest of the family. A placement of *Cassytha* as sister group to *Hypodaphnis*, as in topology 3 of Figure 2, would require a parallel deletion in *Cassytha*. The most likely hypothesis for character #32 is that a 5 bp duplication common to the Magnoliaceae and most Laurales has been lost in a clade comprising the Core Lauraceae, the Mezilaurus group, *Caryodaphnopsis*, and *Neocinnamomum*. A position of *Cassytha* as sister group to *Neocinnamomum*, as in topology 1 of Figure 2, would require a parallel deletion in *Neocinnamomum* (or a parallel duplication in *Cassytha*). Character #38 is a poly-T plus poly-G region, in which the number of T's and G's is highly homoplastic within the Lauraceae. Still this character allows the separation of the Lauraceae except *Hypodaphnis* (with at least two T's and not more than two G's in the central region of uncertain alignment) from all other taxa (with at least three G's and no T's in this region). Therefore, a placement of *Cassytha* as sister group to *Hypodaphnis*, as in topology 3 of Figure 2, would again require a parallel, identical change in either *Cassytha* or *Hypodaphnis*.

The remaining three indels (#4, 7, and 17) are homoplastic in some topologies but not in others. Character #4 is most parsimoniously explained as deletion of a C in a clade comprising the Core Lauraceae, the Mezilaurus group, *Caryodaphnopsis*, and *Neocinnamomum*. As in character #32, topology 1 in Figure 2 would require an additional step. Character #7 is clearly a duplication of a 4 bp motif in all Lauraceae except *Hypodaphnis*. As in character #22, topology 3 in Figure 2 would require an additional step. Character #17 gives additional support to the Magnoliaceae and the Core Monimiaceae as monophyletic groups. With respect to the Lauraceae, it is most parsimoniously explained as a deletion (compared to most taxa) of a 4 bp motif in a clade comprising the Core Lauraceae, the Mezilaurus group, *Caryodaphnopsis*, and *Cassytha* (most likely also *Neocinnamomum*, but the respective part of the sequence is unknown in this genus). A placement of *Cassytha* outside this group, as in topology 3, would again require an additional step.

In summary, mapping the characters derived from indels and regions of uncertain alignment onto the five topologies in Figure 2 adds two steps to topology 1 and four steps to topology 3.

Discussion

As expected, the results of all analyses are congruent in most of their features to those of Rohwer (2000) and Chanderbali et al. (2001), so that it is now possible to place most genera of the Lauraceae within the phylogenetic framework, or at least into a group of closely related taxa. However, the differences among the results of these studies and the analyses presented here shed light not only on the phylogeny of the taxa involved but also on the effects of the different methods of analysis.

Comparison of different methods of phylogenetic analysis

The parsimony analyses were obviously sensitive to long-branch attraction, as their topology changed with the taxon sample. Three genera of the Lauraceae (*Cassytha*, *Hypodaphnis*, and *Neocinnamomum*) show conspicuously long branches (Fig. 1), and the same three genera appear in different positions in the different analyses. The topology of the maximum likelihood and Bayesian analyses, on the other hand, showed no sensitivity to changes in the taxon sample. This certainly enhances their credibility as compared to the parsimony analyses.

Additional evidence comes from the mapping of the informative characters derived from indels or regions of uncertain alignment onto the cladograms. Two additional steps for topology 1 and four additional steps for topology 3, both derived from parsimony analyses of the coding or complete (coding and non-coding) matrices, likewise suggest that the results of the Bayesian and maximum likelihood analyses (which always retrieve the shorter topology 2) may be more reliable.

In the simplified matrices, the results of the Bayesian analyses were generally congruent with those of the maximum likelihood analyses, but the Bayesian analyses yielded support values (posterior probabilities) in about the same time as needed to complete a standard maximum likelihood analysis, without bootstrapping.

Even with the simplified matrices, bootstrap analyses with the optimality criterion set to maximum likelihood proved time-consuming compared to the other methods. In addition, MrBayes 3.0b4 allows using different evolutionary models simultaneously for the coding and the non-coding parts of the complete matrices, in contrast to maximum likelihood (at least in PAUP), where it is necessary to specify a single evolutionary model for the entire

data set. Therefore, we will prefer Bayesian inference in data sets that might be sensitive to long-branch attraction.

COMPARISON OF THE DIFFERENT MATRIX PARTITIONS

Table 5 shows that, contrary to common expectation, the proportion of informative characters is about equal in the coding part of the matrix (the *mat*K gene) and in the non-coding part (ca. 25% in the large matrix, ca. 15% in the simplified matrix). This is probably due to the fact that the number of mutations in *mat*K is substantially greater than in most other genes used in angiosperm systematics, as described in detail by Hilu et al. (2003). Substitution rates in the first and second codon positions in *mat*K approach those of the third position, leading to a relatively high proportion of non-synonymous mutations. As the *mat*K gene is almost twice as long as the non-coding parts of the *trn*K intron, it yields almost twice as many informative characters. It is therefore not surprising that the cladograms resulting from the complete matrix, comprising both the coding and the non-coding region, are largely congruent with those derived from the *mat*K gene alone.

It is, however, surprising that the coding and the non-coding part of the matrix consistently support different topologies. Analyses of the coding (and complete) matrices always result in topology 1 or 2 (or 3 in a single case), where *Hypodaphnis* is a member of the Lauraceae. Analyses of the non-coding matrices, on the other hand, always result in topology 4 or 5, in which *Hypodaphnis* is sister to the Hernandiaceae. The relatively low number of informative characters in the non-coding region would explain a reduced resolution or reduced support for some clades (see Table 4), but it cannot explain the sometimes considerable support for the clade uniting *Hypodaphnis* with the Hernandiaceae (clade X in Fig. 2). In an attempt to find the source of this conflict, we first identified the characters supporting clade X in MacClade. In both the coding and the non-coding region we found three such positions (alignment positions 953, 1209, 1847 and 820, 2520, 2723, respectively), plus an additional position (999) shared by *Hypodaphnis* and *Sparattanthelium* where *Hernandia* has a gap. In the coding region, however, the characters supporting monophyletic Lauraceae (incl. *Hypodaphnis*) are far more numerous, so that their signal overwhelms the signal supporting clade X even in the complete matrix. In the non-coding part, on the other hand, there is no such compensation, so that clade X is retrieved even if only a single of the three characters supporting it is included in the analysis.

In a second step, we tried to reconstruct the folding pattern of the *trn*K intron, following the suggestions of Kelchner (2002), with the aim of creating separate partitions for stem and loop nucleotides. With the help of the sequences given in the appendix of their paper, we were able to identify the main structural domains and some subdomains according to the model of Michel et al. (1989). However, we could not reconstruct the precise folding pattern within the larger domains I (except for several subdomains of less than 50 bp), III, and IV. Submitting the RNA equivalent of a DNA sequence (of *Lindera benzoin*) or usually parts of it (for "domain-by-domain folding" according to Kelchner, 2002) to the MFOLD-server (http://bioweb.pasteur.fr/seqanal/interfaces/mfold-simple.html) returned multiple folding patterns for all but the smallest (sub)domains. None of these patterns agreed completely with the model of Michel et al. (1989) and several appeared equally plausible. None of the characters supporting clade X is located in any of the (sub)domains for which we could reconstruct the structure. Except for the last one (alignment position 2723), they are all located in the largest domain IV, but among the 46 models that MFOLD provided for this domain, we never found any two of these characters in a paired arrangement with each other. Therefore, we decided that reconstruction of the secondary structure was beyond the scope of this paper, although we still assume that the reason for the conflict between the results obtained from coding and non-coding sequences has to be sought in the secondary structure.

In our opinion, the coding part of the sequence (= the *mat*K gene) gives us a better estimate of the phylogeny than the non-coding *trn*K intron sequence. This opinion is based mainly on the observation that the topologies retrieved from the *mat*K gene sequence are in much better agreement with the results from earlier studies of the Laurales using other regions of the genome (Renner, 1999; Renner & Chanderbali, 2000; Chanderbali et al., 2001). We regard not only the position of *Hypodaphnis* as sister to the Hernandiaceae but also the placement of *Peumus* in a clade separate from the other Monimiaceae, as in topology 5 (Fig. 2) of our study, as an artifact. In the studies of Renner (1999) and Renner and Chanderbali (2000), based on six and five genome regions, respectively, *Peumus* is clearly a member of the Monimiaceae, invariably with 100% bootstrap support.

The indel mapping helps to choose among the

different results obtained from the analyses of the coding sequences. Since it adds two steps to topology 1 and four steps to topology 3, we regard topology 2 in Figure 2 as the most likely pattern of phylogeny in the Lauraceae.

THE PHYLOGENETIC POSITIONS OF *CASSYTHA*, *HYPODAPHNIS*, AND *NEOCINNAMOMUM*

In the two previously published phylogenetic analyses of the Lauraceae (Rohwer, 2000; Chanderbali et al., 2001) the hemiparasitic genus *Cassytha* was found in different positions. In the former study, based on partial *mat*K and *trn*K intron sequences, it was almost basal within the Lauraceae, separated from the most basal genus *Hypodaphnis* by a branch that did not receive bootstrap support. In the latter, it was sister to *Neocinnamomum*, as in topology 1 (Fig. 2) of this study. The present study shows that the sub-basal position of *Cassytha* in Rohwer (2000) has been an artifact caused by long-branch attraction, which occurs only under very special circumstances, viz., parsimony analysis of only or at least predominantly coding positions in the absence of *Neocinnamomum* but presence of *Hypodaphnis*. In agreement with the results of Chanderbali et al. (2001), the genus *Cassytha* is indeed nested among the otherwise woody Lauraceae, but not as sister group to *Neocinnamomum*. Instead, it is sister group to a clade including all genera except *Hypodaphnis* and the Cryptocaryeae. This suggests that not only its leafless, hemiparasitic habit but also other aberrant characteristics, such as cellular instead of nuclear endosperm formation, lack of a nucellar cap, and formation of the micropyle by both integuments (Heo et al., 1998), are autapomorphic traits of this genus. They certainly do not justify a separation as a subfamily (Kostermans, 1957) or even family (Lindley, 1836) of its own. Nevertheless, the evolutionary pathway leading to the twining hemiparasitic habit is still enigmatic, as *Cassytha* apparently does not have any closely related living relatives.

The monotypic African genus *Hypodaphnis* was resolved as the basal branch within the Lauraceae in our earlier study (Rohwer, 2000) and in Matrix II of Chanderbali et al. (2001), whereas it was weakly supported as sister to the Cryptocarya group in Matrix I of Chanderbali et al. (2001). In the present study, it is consistently placed as the earliest branch within the Lauraceae in all analyses including the (coding) *mat*K sequences, whereas it is consistently placed as sister group to the Hernandiaceae in all analyses of only the non-coding parts of the *trn*K intron. However, since the non-coding parts of the sequence yielded relatively few informative characters, as described above, a few base pairs that are by chance identical in the two groups might be sufficient to bring them together. On the other hand, there are also morphological and anatomical similarities between *Hypodaphnis* and the Hernandiaceae (see below), so that it would appear possible to consider *Hypodaphnis* as a third evolutionary lineage, between Lauraceae and Hernandiaceae. In the five gene analyses of Renner and Chanderbali (2000) and Chanderbali et al. (2001), however, the inclusion of *Hypodaphnis* in the Lauraceae received moderate to strong (77%–96%) bootstrap support, and the placement of *Hypodaphnis* in the Lauraceae has never been questioned based on morphological evidence.

Although a basal position of *Hypodaphnis* within the Lauraceae has been confirmed by all molecular studies so far (including the present one), it is still somewhat surprising. The inferior ovary used to be considered as an advanced character, and the wood structure was described by Richter (1981) as quite advanced and intermediate between *Eusideroxylon* and the Hernandiaceae. In a way, the genus does occupy such an intermediate position in the phylogenetic tree, but its supposedly advanced characteristics appear plesiomorphic rather than apomorphic in light of the phylogenetic information. In combination with the topology of the Cryptocarya group, in which the *Beilschmiedia*-like genera with freely superior ovaries form a derived clade, this strongly suggests that the free superior ovaries, which characterize the majority of the Lauraceae, are an apomorphic character that has arisen at least twice within the family. If the Hernandiaceae were shown to be the sister group of the Lauraceae, which is still uncertain (see Renner & Chanderbali, 2000), then an inferior ovary would likely be plesiomorphic. Otherwise, the plesiomorphic condition seems to be a superior ovary enclosed in a deeply urceolate receptacle, as in the majority of the Laurales, with several parallel origins of both inferior and freely superior ovaries.

The Asian genus *Neocinnamomum* was lacking in our earlier study, and even now we were unable to obtain a complete sequence from this taxon. The unknown part of the sequence is 490 out of the total 2750 alignment positions long, including 85 positions from the coding and 405 positions from the non-coding part. Filling this gap could, of course, lead to more confidence in the placement of *Neocinnamomum*. In the study of Chanderbali et al. (2001), *Neocinnamomum* is found in a common clade with *Cassytha*, as in the parsimony analyses of the complete and the coding matrices presented

here. However, two informative indels (#4 and 31 in Table 5) are in conflict with this arrangement. The maximum likelihood and the Bayesian analyses rather suggest that *Neocinnamomum* is sister to *Caryodaphnopsis*. While there are no informative indels in the available part of the sequence explicitly supporting or contradicting this relationship, it is supported by a general morphological similarity between the two genera. They agree in having mostly triplinerved leaves that are opposite in *Caryodaphnopsis* and can be subopposite in *Neocinnamomum*, usually tetrasporangiate anthers, in which the four pollen sacs are arranged in a shallow arc (occasionally disporangiate in *Caryodaphnopsis*), and fruits sitting almost free on a rather swollen pedicel. *Cassytha*, on the other hand, is leafless, has disporangiate anthers, and fruits in which the ovary is completely enclosed in an accrescent receptacular tube. Although at least some of the morphological characters common to *Caryodaphnopsis* and *Neocinnamomum* may be plesiomorphic for the entire clade, we are at least certain that *Neocinnamomum* is closer to *Caryodaphnopsis* than to *Cassytha*. It should be noted that the missing part of the sequence includes several informative indels (#11–25 in Table 6), but only one of them (#20) has the potential of being informative with respect to the relationship of *Caryodaphnopsis* and *Neocinnamomum*.

OTHER RELATIONSHIPS WITHIN THE LAURACEAE

As indicated above, this study generally confirms the relationships found in the two previously published phylogenetic analyses (Rohwer, 2000; Chanderbali et al., 2001).

The genera *Aspidostemon*, *Beilschmiedia*, *Cryptocarya* (incl. *Ravensara*, see van der Werff, 1992), *Endiandra*, *Eusideroxylon*, *Potameia*, and *Potoxylon* (not examined here, but in Chanderbali et al., 2001) form the clearly monophyletic Cryptocarya group, which may be formally recognized as tribe Cryptocaryeae. Within this group, the genus *Beilschmiedia* is clearly paraphyletic in its current circumscription, with respect to *Endiandra* and *Potameia*. Further studies are necessary to decide whether *Beilschmiedia* should be split into smaller entities or enlarged to include the latter two genera. The genera *Brassiodendron* and *Triadodaphne*, which both were included in *Endiandra* (the former by Kostermans, 1957, and Hyland, 1989, the latter by Rohwer, 1993) can safely be placed in *Beilschmiedia* s.l., although they have not been studied with molecular markers yet. The rare South African *Dahlgrenodendron* and the possibly extinct Malaysian *Hexapora* most likely also belong to the Cryptocarya group.

The Neotropical genera *Anaueria*, *Chlorocardium*, *Mezilaurus*, *Sextonia*, and *Williamodendron* invariably occupy a position between *Caryodaphnopsis* (with or without *Neocinnamomum*) and the group that is called Core Lauraceae in this study, but some of them are very dissimilar morphologically and they do not always form a well-supported monophyletic group. Invariably well supported is a close relationship of *Mezilaurus*, *Sextonia*, and *Williamodendron*; the latter has even been included in *Mezilaurus* by van der Werff (1987). They share leaves that are usually crowded at the tips of the branchlets, botryoid or dibotryoid inflorescences, and a deeply urceolate receptacle. In addition, *Mezilaurus* and *Williamodendron* have rather small, flat, mostly more or less discoid cupules. Their flowers, however, are quite different. While *Mezilaurus* and *Williamodendron* share flowers with three fertile stamens, each with two (*Mezilaurus*) or four (*Williamodendron*) pollen sacs, *Sextonia* has nine fertile stamens that are laminar and papillose, each with four pollen sacs that are introrse in the two outer whorls. This structure is reminiscent of a group currently classified as *Ocotea* subg. *Dendrodaphne*, and therefore *Sextonia* was considered a member of this group until van der Werff (1997), supported by the anatomical differences discovered by Richter (1981), raised it to generic rank. Sister to these three Mezilauroid genera (*Mezilaurus*, *Sextonia*, and *Williamodendron*) is most likely a clade including *Anaueria* and *Chlorocardium*. While this clade appears in only some of our analyses, with rather weak or no support, it was well supported in the ITS and five gene analyses of Chanderbali et al. (2001). The two genera share opposite leaves (possibly a plesiomorphic character?), but have very different flowers. Therefore, *Anaueria* has even been included in *Beilschmiedia* by Kostermans (1957), whereas *Chlorocardium* has been treated as *incertae sedis* by Rohwer (1993). In the wood structure, however, Richter (1981) recognized close similarities between *Anaueria* and *Mezilaurus*.

Nearly all genera that have not been discussed so far belong to a group with surprisingly low genetic divergence among its members in all markers examined so far except ITS (see Chanderbali et al., 2001), the Perseeae–Laureae clade of Chanderbali et al. (2001) or Core Lauraceae of this study. Within this group, the genera *Alseodaphne*, *Apollonias*, *Dehaasia*, *Nothaphoebe* (not examined here, but included in *Persea* by Kostermans, 1957), *Persea* (incl. *Machilus*), and *Phoebe* (not examined here but in both earlier publications) constitute the Per-

sea group. This group has been recognized in both previous molecular studies (Rohwer, 2000; Chanderbali et al., 2001) and in several of the analyses presented here, although with varying levels of support. Although the Persea group as a whole is certainly monophyletic, it needs to be studied in more detail, because the available data suggest that *Persea* might not be monophyletic in its current circumscription. Nearly all of the remaining genera, even those that have not yet been studied with molecular markers (*Gamanthera*, *Phyllostemonodaphne*), clearly belong to the group called the Laureae–Cinnamomeae group in this paper. It includes the former Laureae and the Aniba and Ocotea subgroups of Rohwer (1993), except *Neocinnamomum* (see above). This rather complex group poses numerous taxonomic problems, since both morphological and molecular evidence suggest that several of the larger genera within this group (*Cinnamomum*, *Endlicheria*, *Lindera*, *Litsea*, *Nectandra*, *Ocotea*, and *Rhodostemonodaphne*) are not monophyletic in their current circumscription (Chanderbali et al., 2001, and unpublished data). Although the Lindera–Litsea complex has been investigated by Li et al. (2004) and the Cinnamomum complex by Groth et al. (unpublished data), we are still far from understanding most of the relationships within this group. Although a molecular clock is not applicable in our data, due to enormously different branch lengths, the inclusion of *Sassafras* among the Core Lauraceae strongly suggests that this genus originated in one of the more recent radiations within the family. Chanderbali et al. (2001) estimated the age of the radiation within this clade as 44 ± 7 Mya, which currently appears to be the best estimate available. *Sassafrasoxylon gottwaldii* from the Late Cretaceous of Antarctica (Poole et al., 2000), therefore, may have to be interpreted as a case of striking convergence to *Sassafras* in a seasonal climate rather than evidence for a Gondwanan origin of this genus.

The only genus that currently cannot at all be placed within the phylogenetic framework described above is the Asian *Cinnadenia*. Its flower structure is so aberrant that it has been treated as *incertae sedis* by Rohwer (1993). Unfortunately, we have not been able so far to obtain material of this genus from which it was possible to extract sufficiently intact DNA.

In summary, the results confirm that the monotypic African genus *Hypodaphnis* is sister to all other Lauraceae, as in Rohwer (2000) and figure 1 of Chanderbali et al. (2001), and that the parasitic genus *Cassytha* is nested among the otherwise woody Lauraceae, in a position similar to that found by Chanderbali et al. (2001). The sub-basal position of *Cassytha* found in our earlier analysis (Rohwer, 2000) was clearly an artifact. Judged from the distribution of informative indels, Bayesian inference apparently yields more plausible results than parsimony. If this is correct, then our results also suggest that *Neocinnamomum* is indeed close to *Caryodaphnopsis*, as morphology would suggest, not sister to *Cassytha*, as in the parsimony analyses of Chanderbali et al. (2001). Further studies in the Lauraceae, using more variable markers, will be necessary to resolve the relationships within *Beilschmiedia* s.l. (including *Endiandra* and *Potameia*), and especially within the Core Lauraceae.

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A PHYLOGENETIC STUDY OF THE NEW WORLD *CLEOME* (BRASSICACEAE, CLEOMOIDEAE)[1]

Lupita Sánchez-Acebo[2]

ABSTRACT

This study was designed to investigate phylogenetic and morphological relationships within *Cleome*, focusing on the South American species. Relationships were inferred from the chloroplast genomic *trn*H-*psb*A. Phylogenetic analyses support the monophyly of *Cleome* and the recognition of three clades within it, which are supported morphologically by seed and pollen characters. The African clade contains only African species (Old World); the Andean and Tarenaya clades include all the New World species, most of which are distributed in South America. The well-suported Andean clade groups the Andean species and contains *Podandrogyne* nested within it. The Tarenaya clade is formed mostly by species of the spiny section *Tarenaya*. Although there is little resolution in the deeper nodes of the phylogeny, the results do suggest that some sections/groups are not monophyletic. In general, seed and, to a lesser extent, pollen characters were found to be systematically useful within *Cleome*.

Key words: Brassicaceae, *Cleome*, Cleomoideae, phylogenetics, pollen, seed, *trn*H-*psb*A.

Cleomoideae and Capparoideae were previously included in Capparaceae (Cronquist, 1968, 1988; Thorne, 1976, 1983; Dahlgren, 1980; Takhtajan, 1980, 1997). However, morphological and molecular studies (Rodman, 1991a, 1991b; Rodman et al., 1993, 1994, 1996, 1998; Chase et al., 1993; Judd et al., 1994) suggest that Capparaceae so delimited are paraphyletic; hence Capparaceae have been included in Brassicaceae s.l. by some authors (Stevens, 2001; Judd et al., 2002; APG, 1998, 2003). However, Cleomoideae, Capparoideae, and Brassicoideae all form well-supported monophyletic clades (Hall & Sytsma, 2000, 2002; Hall et al., 2002) and could be recognized as three separate families, the Capparaceae, Cleomaceae, and Brassicaceae, a course of action recommended by some recent authors (Hall et al., 2002).

Here I discuss phylogenetic and morphological relationships within *Cleome* L. (Cleomoideae), focusing on the South American species. *Cleome* is the largest genus of the subfamily Cleomoideae, comprising 180 to 200 species distributed primarily in tropical and subtropical Africa, America, Asia, and Australia; a few species are weedy and pantropical in distribution (Iltis, 1952; Vanderpool, 1989; Mabberley, 1997). *Cleome* is comprised of small to large herbs or woody shrubs, with 3- to 13-foliolate palmately compound (rarely unifoliolate) leaves, and well-defined racemose, bracteate or ebracteate inflorescences (occasionally with solitary flowers). The flowers are 4-merous, weakly to strongly zygomorphic, perfect, typically with six stamens, a short to elongate gynophore on which the ovary is borne, and a nectariferous disk between the calyx and stamens that is rudimentary or fleshy. The fruit is a bi-carpellate septicidal many-seeded silique with a replum (persistent placenta) that lacks the connecting septum of Brassicoideae.

Pax and Hoffman (1936) divided *Cleome* into two sections, four subsections, and six series, using leaf division, habit, and stamen number. Their classification was largely based on characters that were not reliable taxonomically because of their great variability within the genus. The most extensive, although still unpublished, study of the genus was that of the New World species of *Cleome* by Iltis (1952). He recognized a total of 58 species and 29 subspecies and used characters of the seed, nectary

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[2] Museo de Historia Natural Noel Kempff Mercado, Casilla 2489, Santa Cruz, Bolivia, and Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166, U.S.A. lupita.sanchez@mobot.org.

disk, raceme morphology, floral aestivation, and leaves (in that order of importance) to divide New World *Cleome* into two subgenera, 10 sections, and 17 series. Since most of his classification has not been published, a system of informal names corresponding to the infrageneric taxa of Iltis (1952) is presented here (Table 1) and will be followed throughout the present discussion.

Three of the ten sections/groups recognized by Iltis (*Ranmanissa*, *Gymnogonia*, and *Rutidosperma*) are introduced to the New World and belong to the Old World supergroup; the other seven are endemic to the Western Hemisphere and belong to the New World supergroup. A few New World species of section *Tarenaya*, e.g., *Cleome aculeata* and *C. parviflora* (for authorities of names used here, see Table 1), have been introduced into the Old World, and one, *C. afrospina* Iltis (Iltis, 1967), is a West African native.

Of the seven New World sections/groups recognized by Iltis (1952), section *Tarenaya* is the largest. Iltis thought that it was the most primitive of the New World sections because of its distinctive seeds with a large central cleft, a putatively primitive condition. Section *Tarenaya* has 24 species, arranged in eight subgroups, and includes the popular cultivated *Cleome hassleriana* (*C. spinosa* Hort.), the Spider Flower. The embryo, like the seed, is curved, as in other Cleomoideae. The seeds of section *Tarenaya* are distinctive because of the usually thin membrane connecting the cotyledonar and radicular "claws" of the horseshoe-shaped testa and the distinctive internal "cleft cavity," the space between the cotyledonar and radicular "claws" of the embryo, which is unusually large when seen in cross section (Iltis, 1967). The presence of the membranes joining the cotyledonar and radicular claws of the seed suggested to Vanderpool (1989) that section *Tarenaya* (South America) was probably a sister of the North American group, which also has this feature, even though the cleft cavity there is all but suppressed. The nectariferous disk is rudimentary, or usually only slightly developed and conic or disciform. Most species are characterized by the presence of typically paired, stipular prickles that can be straight or curved and hooked.

Apart from Iltis's unpublished and now rather venerable thesis of the New World *Cleome*, there have been few systematic studies of the genus *Cleome* as a whole (cf. Iltis, 1957, 1959, 1967; Vanderpool, 1989). Its taxonomic limits are unclear, and both morphological and molecular data suggest a sister relationship between *Cleome* and *Polanisia* (Iltis, 1958) and the inclusion of *Podandrogyne* within *Cleome* s.l. (Hall et al., 2002; Iltis & Cochrane, 1989). A few floristic treatments of *Cleome* have recently been published, e.g., accounts for the *Flora of the Venezuelan Guayana* (Ruiz-Zapata & Iltis, 1998) and *Flora de Nicaragua* (Iltis, 2001). The seed morphology (Ruiz-Zapata & Escala, 1995) and pollen morphology (Ruiz-Zapata & Xena de Enrech, 1997) of some Venezuelan species have been examined. Apart from a study of the phylogeny of Brassicaceae s.l. (Hall & Sytsma, 2000; Hall et al., 2002) that includes five species of *Cleome*, there have been no molecular or morphological phylogenetic studies of the genus.

A phylogenetic hypothesis of relationships within *Cleome* is an essential preliminary for any understanding of its diversification. The present study has two main goals: (1) to use chloroplast sequence data to construct a hypothesis of the phylogenetic relationships of the New World species of *Cleome*. This will allow us (1a) to assess the validity of the infrageneric classification of Iltis (1952); (1b) to test the monophyly of *Cleome* sect. *Tarenaya* and to investigate relationships among species of this section; and (2) to study morphological evolution, particularly of seed and pollen characters, within *Cleome* in a phylogenetic context.

Materials and Methods

Taxon Sampling and Sources of Plant Material

A total of 37 species was sampled for molecular phylogenetic analysis, chosen carefully from among Iltis's infrageneric groups (Table 1), including at least one species per section/group. Species from each subgroup of section *Tarenaya* (excluding subgroups G and H) were studied. *Podandrogyne macrophylla* and *P. brachycarpa* were initially included as outgroups, although they came out nested within the *Cleome* Andean group, as was predicted by Iltis and Cochrane (1989). Preliminary morphological cladistic analyses (Rodman, 1991a, b; Judd et al., 1994) and a combined *ndh*F and *trn*L-*trn*F analysis (Hall et al., 2002) suggest *Polanisia* as sister to *Cleome* s.l. *Polanisia dodecandra* was used as an outgroup in the present analyses.

Leaf samples in silica gel were collected in Bolivia and Venezuela. Fresh material was collected from plants growing in a greenhouse at the Missouri Botanical Garden. Herbarium material was taken from specimens deposited in MO, LPB, and USZ (see Appendix 1 for voucher information).

DNA EXTRACTION, AMPLIFICATION, AND SEQUENCING

Total DNA was extracted from fresh leaves, leaves dried in silica gel, or herbarium material. Extractions from fresh and silica material were made using a modified CTAB (small-scale) protocol (Doyle & Doyle, 1987). Extractions from herbarium material were made using the protocol of Doyle and Doyle (1987), but instead of the last step (where the DNA is precipitated with NaOAc and ice-cold 95% ethanol, rinsed with 70% ethanol, and resuspended with Tris-HCl), the DNA was further purified using the methods contained in the QIAquick PCR purification kit (Qiagen, Inc., Valencia, California).

The chloroplast non-coding region *trn*H-*psb*A (Hamilton, 1999) was chosen for DNA sequencing because it showed high variability among species of *Cleome*. The non-coding region of the *trn*L gene (Tarberlet et al., 1991) did not show sufficient variation. The fragments of DNA were amplified using the standard PCR (Polymerase Chain Reaction) technique. Each reaction of 50 µl contained 35 µl ddH_2O, 5 µl 10× reaction buffer, 5 µl 25 mM $MgCl_2$, 0.5 µl 10 mM dNTP, 1.5 µl 10 mM of each primer (*trn*H and *psb*A), 0.5 µl *Taq* DNA Polymerase, and 1 µl DNA template. Reactions were run on a PTC-200 Thermal Cycler (MJ Research) with an initial 3 min. denaturation at 94°C, followed by 35 cycles of 30 sec. at 94°C, 30 sec. at 53°C, and 45 sec. at 72°C. The reaction was completed with a final 7 min. extension at 72°C, and then held at 4°C.

PCR products were purified using the QIAquick PCR purification kit (Qiagen, Inc.). Purified PCR products were sequenced using a BigDye Terminator Cycle sequencing kit (Applied Biosystems). Each reaction of 10 µl contained 2 µl 2.5× sequencing buffer, 2 µl 1–10 mM *trn*H or *psb*A primers, 1 µl Big Dye, 1–4.5 µl ddH_2O, and 0.5–4 µl DNA template. For some species, 0.5 µl 20% DMSO (dimethyl sulfoxide) was added to the sequencing reactions. Sequencing reactions were analyzed on an ABI Prism 377 automated DNA Sequencer (Applied Biosystems).

Chromatograms were assembled and edited using Seqman version 4.0 (DNASTAR Inc., Madison, Wisconsin). Sequence alignment was initially performed using ClustalX (Thompson et al., 1997) with the default parameters and verified and modified manually with Se-Al 1.d1 software (Rambaut, 1996). The *trn*H-*psb*A region has a high frequency of indels (these are from 1 to 290 bp in length in *C. gynandra* from South America), making the alignment ambiguous in some areas. All ambiguous areas were excluded from the analyses, and indels that were not phylogenetically informative were scored as missing data. Indels that were informative (i.e., indels of the same size and position that were present in more than one taxon) were added as presence/absence data at the end of the matrix using MacClade 4 (Maddison & Maddison, 2000) and were scored following the method of Simmons and Ochoterena (2000).

PHYLOGENETIC ANALYSES

Maximum parsimony (MP) and maximum likelihood (ML) analyses were performed using PAUP*4.0b10 software (Swofford, 2000). Under Fitch parsimony (Fitch, 1971), trees with and without scored indels were generated using the heuristic search option with tree-bisection-reconnection (TBR) branch swapping, 100 random addition replicates, Multrees and ACCTRAN options in effect, MAXTREES set to automatically increase by 100, and gaps treated as missing data. Confidence of clades of the resulting topology was estimated by bootstrap analysis (Felsenstein, 1985), using 300 bootstrap replicates, MAXTREES set to 1500, and 10 random addition replicates. Two separate analyses were performed on the data set, one excluding indels and a second with indels (scored as presence/absence) included. In both analyses, six species were excluded, four (*Cleome boliviensis, C. dendroidea, C.* sp. nov. aff. *pernambucensis* (Costa e Sylva, 2000), and *C. rutidosperma* from Africa) that had incomplete sequences and two species (*C. gynandra* from South America and *C. stenophylla*) that had large deletions.

Maximum likelihood analysis was performed using the data set with indels excluded. PAUP* and Modeltest (Posada & Crandall, 1998) were employed to evaluate and identify the model of evolution that best fit the data, using a randomly chosen MP tree as the starting tree. The heuristic search of the ML analysis using the parameters of the TVM+G model selected by Modeltest consisted of five random addition sequence replicates with TBR branch-swapping and Multrees in effect.

MORPHOLOGICAL CHARACTERS

Seeds and pollen

Seeds and pollen of all species included in the phylogeny were obtained from herbarium specimens (see voucher references in Appendix 1). Entire seeds and longitudinal hand sections of the seeds were examined using a Nikon SM2645 ste-

Table 1. Species of *Cleome* included in this study; they have been organized into an informal classification, based on the unpublished classification of Iltis (1952). Supergroups, groups, and subgroups are comparable to subgenera, sections, and series of Iltis (1952), respectively: Old World supergroup = subgenus Eucleome, New World supergroup = subgenus Neocleome; Andean group = section Andinocleome (subgroup A = series Chilensis, subgroup B = series Pilosae, and subgroup C = series Fruticosae), North American group = section Peritoma, Ebracteate group = section Melidiscus, and Winged group = section Pterosperma. Within the Tarenaya section: subgroup A = series Serratae, subgroup B = series Speciosae, subgroup C = series Aculeatae, subgroup D = series Roseae, subgroup E = series Spinosae, and subgroup F = series Dendroideae. Numbers in parentheses refer to numbers of species, A = America (NA + CA + SA), AF = Africa, AU = Australia, CA = Central America, NA = North America, SA = South America, An = Andean. In several cases validly published sectional names (i.e., sects. *Ranmanissa*, *Gymnogonia*, *Rutidosperma*, *Tarenaya*, and *Physostemon*) are retained and are not given informal group names.

Supergroup	Section/Group	Subgroup	Species studied	Geography
Old World	*Ranmanissa* (Endl.) Griseb. (1)		*C. viscosa* L.	AU (widespread)
	Gymnogonia R. Br. ex Schult. (1)		*C. gynandra* L. (South America)	AF (widespread)
	Rutidosperma Iltis (1)		*C. rutidosperma* DC. (South America)	AF (widespread)
			C. rutidosperma DC. (Africa)	AF (widespread)
			C. monophylla L.	AF
New World	Andean (8)	Subgroup A (1)	*C. chilensis* DC.	SA
		Subgroup B (1)	*C. pilosa* Benth.	A
		Subgroup C (6)	*C. lechleri* Eichler	An
			C. moritziana Klotzch ex Eichler	An
			C. anomala HBK	An
	North American (6)		*C. sparsifolia* S. Watson	NA
	Tarenaya (Raf.) Iltis (24)	Subgroup A (2)	*C. paludosa* Eichler	SA
		Subgroup B (1)	*C. speciosa* Raf.	CA (Mexico)
		Subgroup C (6)	*C. microcarpa* Ule	SA
			C. diffusa Banks ex DC.	A
			C. aculeata L.	SA (widespread)
			C. cordobensis Eichler ex Griseb.	SA
			C. tucumanensis Iltis	SA
			C. crenopetala DC.	SA
		Subgroup D (1)	*C. rosea* Vahl ex DC.	SA
			C. sp. nov. affinis *pernambucensis*	SA
		Subgroup E (11)	*C. titubans* Speg.	SA
			C. brasiliensis Weinm.	SA
			C. parviflora HBK	A
			C. psoraleaefolia DC.	SA
			C. spinosa Jacq.	A
			C. werdermannii A. Ernst	SA
			C. hassleriana Chod.	SA
			C. chapalaensis Iltis	SA
			C. boliviensis Iltis	SA
		Subgroup F (1)	*C. dendroidea* Schult. f.	SA
	Ebracteate (2)		*C. viridiflora* Schreb.	A
			C. arborea HBK	SA
	Winged (1)		*C. stylosa* Eichler	An
	Physostemon (Mart. ex Zucc.) Iltis (12)		*C. stenophylla* Klotzch ex Urb.	SA

Table 1. Continued.

Supergroup	Section/Group	Subgroup	Species studied	Geography
Outgroup			*Podandrogyne brachycarpa* (DC.) Woodson	SA
			Podandrogyne macrophylla (Turcz.) Woodson	SA
			Polanisia dodecandra (L.) DC.	NA

reomicroscope. Pollen of each species was acetolyzed (Erdtman, 1952) and separated into aliquots for examination by light microscopy and SEM (scanning-electron microscopy). Semipermanent samples for light microscopy were mounted in glycerin gel, sealed with transparent fingernail polish, and observed in an Olympus BX40 light microscope. Seed and pollen samples for SEM analysis were mounted on aluminum stubs, coated with gold, and examined with an Amray Model 1000 SEM. Pictures of seed ornamentation, seed anatomy, and pollen ornamentation were taken for all species studied.

Results

PHYLOGENETIC ANALYSES

Raw length of individual sequences varied between 345 bp (*Cleome titubans*) and 452 bp (*C. brasiliensis*). The total length of the *trn*H-*psb*A region after alignment was 545 bp, but because of ambiguous alignments, 144 (26.2%) nucleotide positions (1–4, 41–57, 103–124, 175–181, 351–390, 412–414, 420–453, 480–487, 537–545) were excluded from all analyses (Table 2). The first analysis, in which indels were not included, yielded 82 (20.4%) informative substitutions and generated four islands of 1498 trees with a length of 219, CI = 0.721, RI = 0.796, and RC = 0.574. In the second analysis with indels included, 93 (22.5%) characters were parsimony-informative. The MP analysis resulted in 11 islands of 357 trees with a length of 241, CI = 0.705, RI = 0.806, and RC = 0.569. Inclusion of indels does affect the topology of the tree, but it caused very few changes in the bootstrap values (cf. Figs. 1 and 2). Comments in the discussion will be based on the strict consensus tree of both analyses. *Polanisia* was designated as outgroup, based on its sister relationship with *Cleome* in previous morphological and molecular studies.

The ML analysis of the 34 species with complete sequences produced a single tree (ln L = −1782.16716) with topology slightly different from the strict consensus trees (see Fig. 3, Table 2). The model that best fit the data is TVM+G (transversional model plus gamma). The topologies produced by the MP and ML analyses indicate that *Cleome*, including *Podandrogyne*, is monophyletic (Figs. 1–3), though with very little bootstrap support (not shown). Within *Cleome* there are three clades, one of them consisting of African species (African clade, Old World species), with 77% and 66% (indels included) bootstrap support. The second clade (Andean clade, Andean species), with 99% bootstrap support, includes members of the Andean group and the segregate genus *Podandrogyne*. The third clade, with rather less support (51%, or 64% with indels included), corresponds largely to section *Tarenaya* (Tarenaya clade, South American species) plus *Cleome arborea*, *C. viridiflora* (Ebracteate group, South America), *C. stylosa* (Winged group, South America), *C. sparsifolia* (North American group, North America), and *C. gynandra* (sect. *Gymnogonia*, Africa). The Andean and Tarenaya clades include all New World species (plus *C. gynandra* of Africa) and are supported as sister clades with 61% bootstrap support in the analysis with indels included (see Fig. 2).

Within the Tarenaya clade, there are several small clades with more than 80% bootstrap support (see Figs. 1, 2). The three species of subgroup C of section *Tarenaya* form the well-supported Arillate clade (84% bootstrap, 94% indels included). The two species of the Ebracteate group plus the single species of the Winged group form another clade (Ebracteate clade) with 100% bootstrap support. A third clade is the Spinosa clade, with 99% bootstrap support (100% indels included), which includes four species of subgroup E (sect. *Tarenaya*). The Spinosa clade may be, in turn, sister to the closely related, large-flowered, spiny *Cleome chapalaensis* (53% support, 62% indels included), as suggested by Iltis (1998). The fourth well-supported clade is the Parviflora clade (100% support), which includes another three species of subgroup E (sect. *Tarenaya*). In addition, there are three other clades of two species each, but mostly with only

Table 2. Alignment information and characteristics of the maximum parsimony and maximum likelihood analyses.

Data set	*trn*H-*psb*A
Number of taxa	34
Raw length (bp)	345–452
Aligned length (bp)	545
Length of indels (bp)	1–29
Characters excluded	144
Variable sites (%)	134 (33.4%)
Parsimony-informative sites (%)	82 (20.4%)
	93 (22.5%) indels included
ML parameters with TVM+G model	
Base frequencies:	
A	0.4334
C	0.1417
G	0.1169
T	0.3080
Substitution rates:	
A-C	0.5098
A-G	0.7157
A-T	0.1542
C-G	0.7898
C-T	0.7157
G-T	1.0000
Proportion of variable sites	0
Gamma distribution shape parameter	0.9359

moderate support. The association of *C. diffusa* and *C. crenopetala* (subgroup C, sect. *Tarenaya*) has 72% support (77% indels included), that of *C. sparsifolia* (North American group) and *C. gynandra* from Africa (Old World sect. *Gymnogonia*) has 65% support (69% indels included), and that of *C. paludosa* plus *C. speciosa* (subgroup A and B, sect. *Tarenaya*) has 45% support (65% indels included).

MORPHOLOGICAL CHARACTERS

Seeds

Cleome has a strongly curved and nearly circular seed, more or less horseshoe-shaped and completely surrounded by a hard testa, with a small and narrow or large and spherical space referred to as the "cleft" between the cotyledon and the radicle of the embryo. The two ends of this "horseshoe" are referred to as "claws" (Iltis, 1952, 1967). The cleft can be completely open or can be partially or completely covered by a membrane connecting the two claws, or the cleft can be completely collapsed by a fusion of the testa of the claws. The interior portion of the cleft, the "cleft cavity," is revealed in a longitudinal section of the seed, where one can see that it forms an invagination of the testa halfway dividing the two ends of the embryo within. The cleft cavity is large and rounded or relatively small and narrow. In several groups of species, the connecting membrane is deeply invaginated diagonally or horizontally, dividing the cleft into an open outer end and a small inner, hidden, cavity. The seeds of *Cleome* are laterally flattened (the 2 "faces" of the seed) and spherical (e.g., *C. monophylla*, Fig. 4A), subspherical (e.g., *C. lechleri*, Fig. 4B), obovoid (e.g., *C. sparsifolia*, Fig. 4C), or cochleate-reniform (e.g., *C. microcarpa*, Fig. 4D).

Seed ornamentation varies greatly. It may be finely to obscurely longitudinally striate and slightly ridged (e.g., *C. monophylla*, Fig. 4A) to strongly transversely ridged (e.g., *C. rutidosperma*, Fig. 4E). In species with transverse ridging, there may be hard excrescences on the ridges (e.g., *C. tucumanensis*, Fig. 4F; *C. microcarpa*, Fig. 4D). In other species, the seed ornamentation is slightly verrucose (e.g., *C. anomala*, Fig. 5A), smooth (e.g., *C. viridiflora*, Fig. 5B; *C. chilensis*, Fig. 5C), reticulate (e.g., *C. chapalaensis*, Fig. 5D), scurfy (e.g., *C. psoraleaefolia*, Fig. 5E), or colliculate and often mottled (e.g., *C. sparsifolia*, Fig. 4C). In one species, the seeds are winged (e.g., *C. stylosa*, Fig. 5F). The wing is composed of greatly enlarged and elongated cells of "blisters" or tubercles, which are flattened and stuck together into a unique circular structure

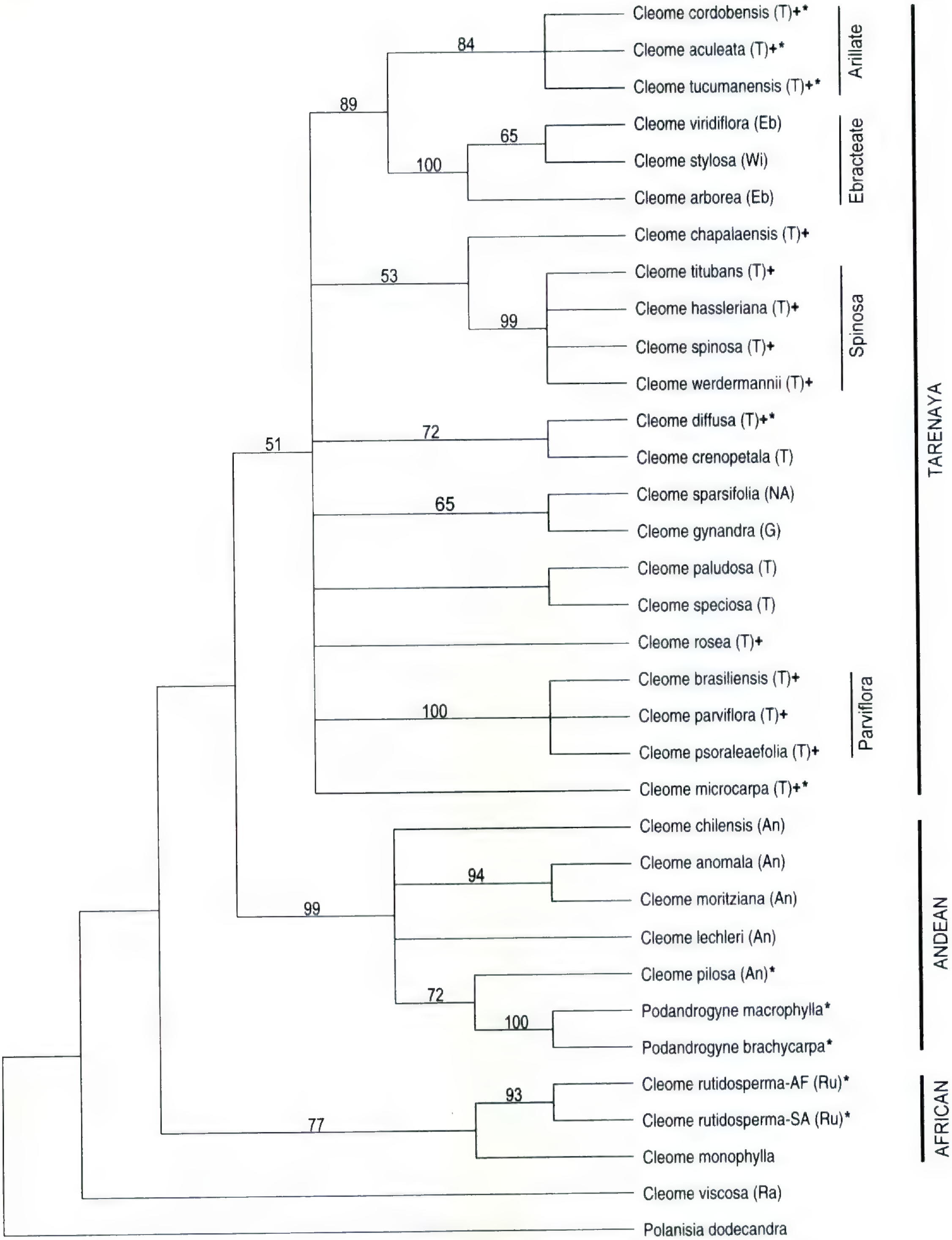


Figure 1. Strict consensus of 1498 maximum-parsimony trees (CI = 0.721, RI = 0.796, RC = 0.574) with indels excluded, bootstrap support above the branches. Letters in parentheses refer to the sections/groups of Iltis (1952): An = Andean group, Eb = Ebracteate group, G = Gimnogonia section, NA = North American group, Ra = Ranmanissa section, Ru = Rutidosperma section, T = Tarenaya section, Wi = Winged group; AF = African, SA = South American. Taxa with stipular prickles are shown with a cross (+), and asterisks (*) indicate taxa with arillate seeds.

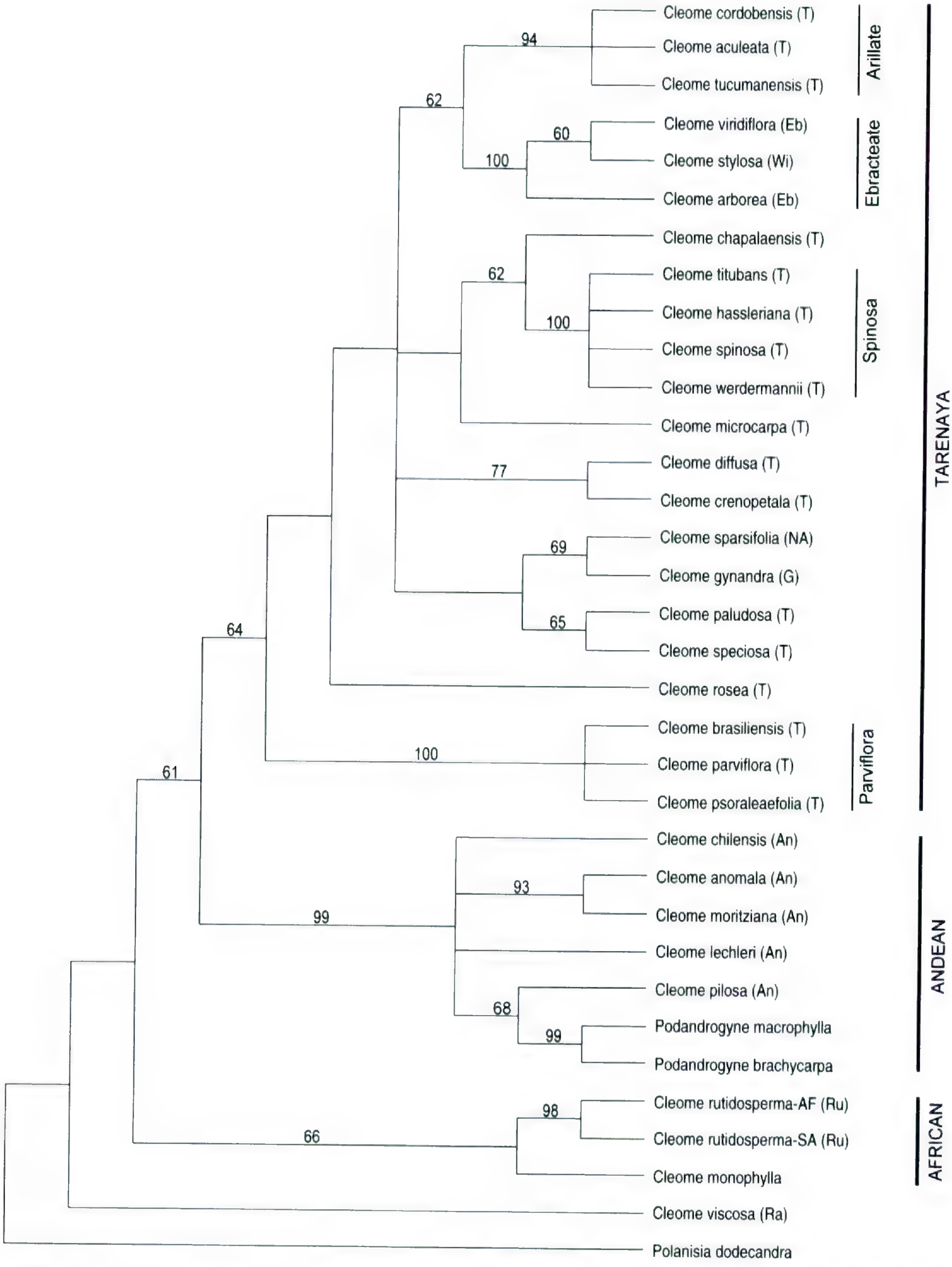


Figure 2. Strict consensus of 357 maximum-parsimony trees (CI = 0.705, RI = 0.806, RC = 0.569) including indels, bootstrap support above the branches. Letters in parentheses refer to the sections/groups of Iltis (1952): An = Andean group, Eb = Ebracteate group, G = Gimnogonia section, NA = North American group, Ra = Ranmanissa section, Ru = Rutidosperma section, T = Tarenaya section, Wi = Winged group. AF = African, SA = South American.

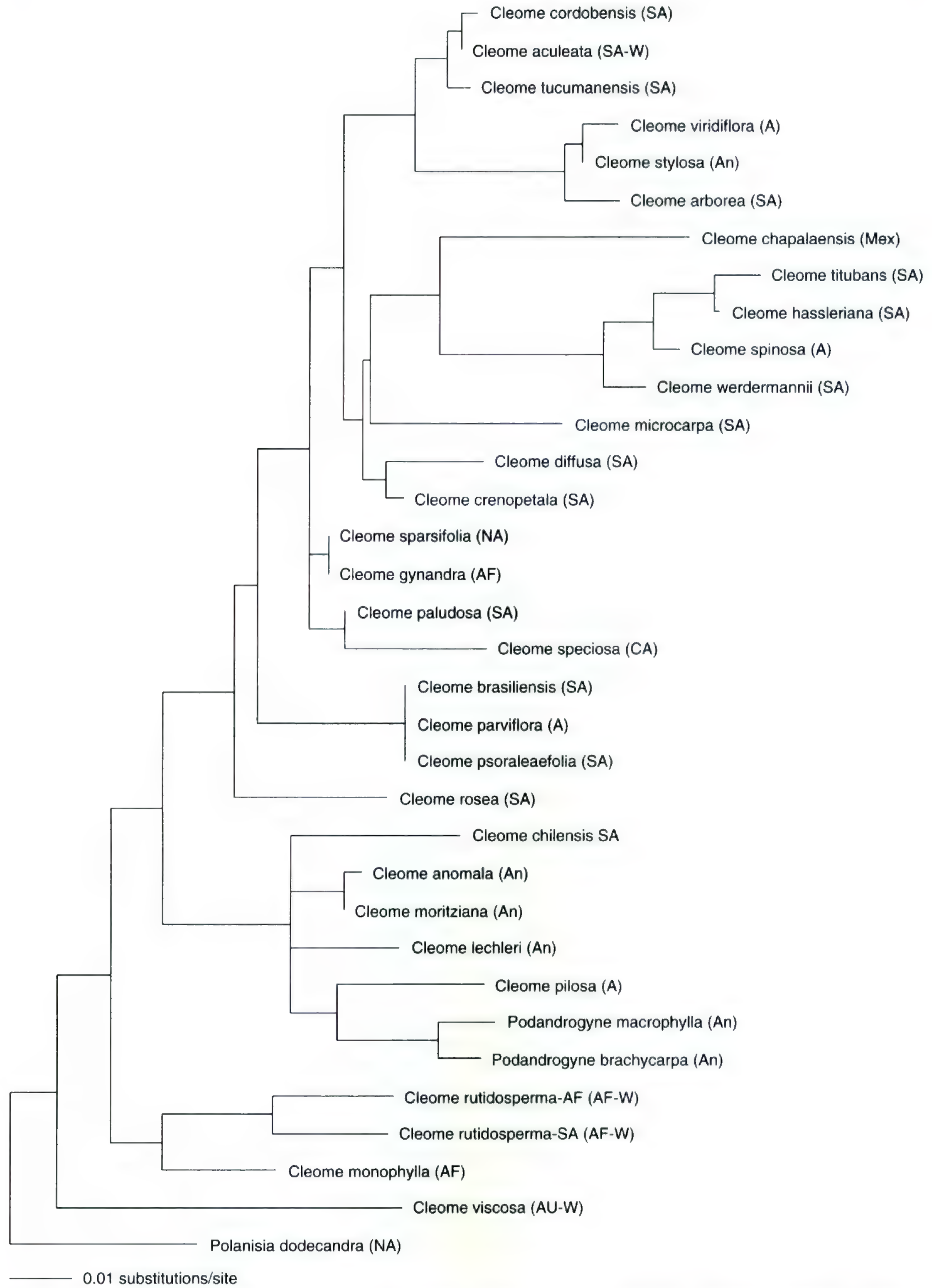


Figure 3. Maximum-likelihood tree under the TVM+G model, −ln = 1782.16176, topology somewhat similar to that of the strict consensus maximum-parsimony tree (Fig. 2). Geographical distribution is mentioned in parentheses after taxa names: A = America (NA+CA+SA), AF = Africa, AU = Australia, NA = North America, SA = South America, W = Worldwide, An = Andes, Mex = Mexico.

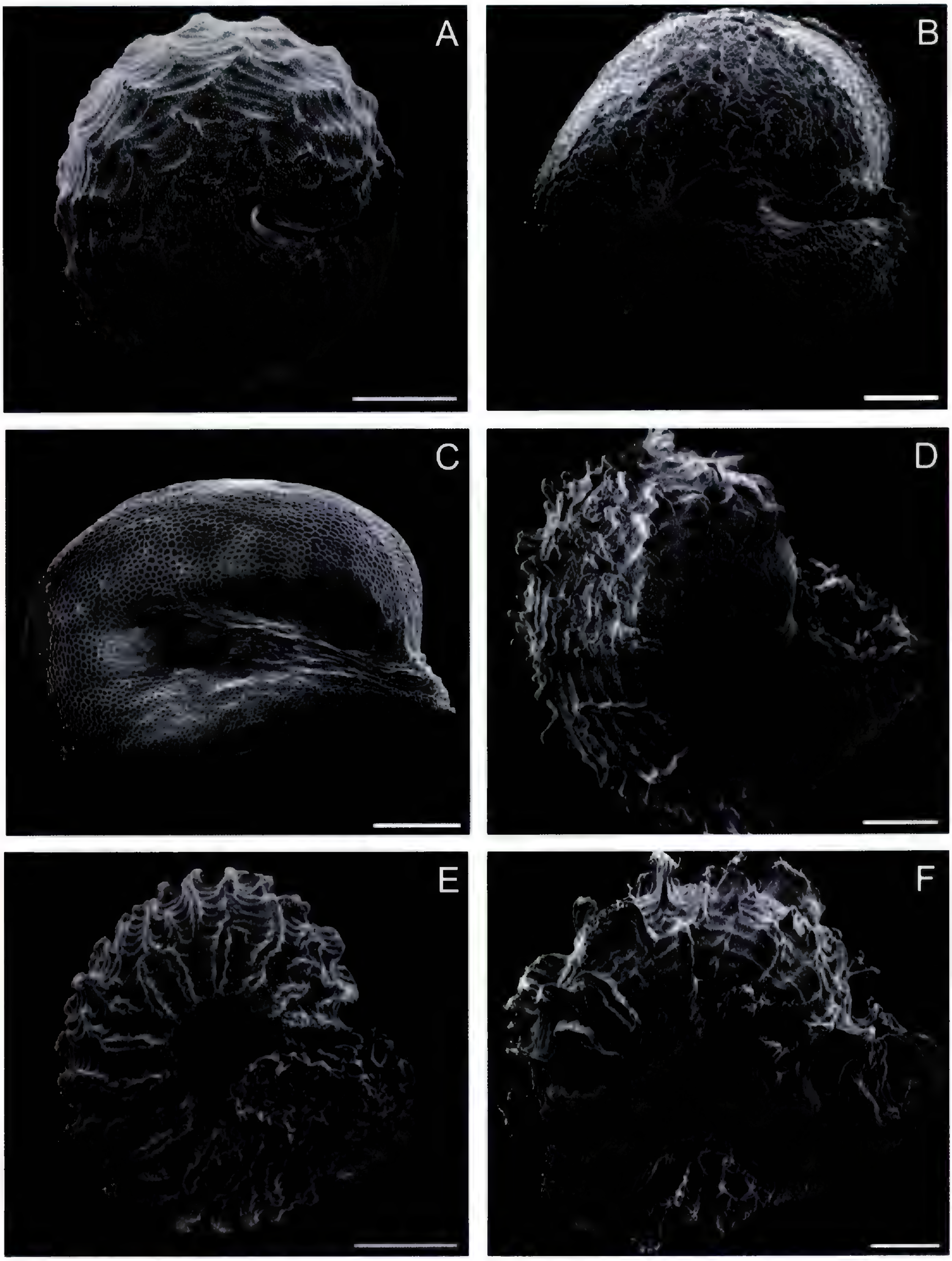


Figure 4. SEM micrographs of seeds showing shapes and surfaces. —A. *Cleome monophylla*. —B. *C. lechleri*. —C. *C. sparsifolia*. —D. *C. microcarpa*. —E. *C. rutidosperma*. —F. *C. tucumanensis*. Scale: A–F = 500 μm.

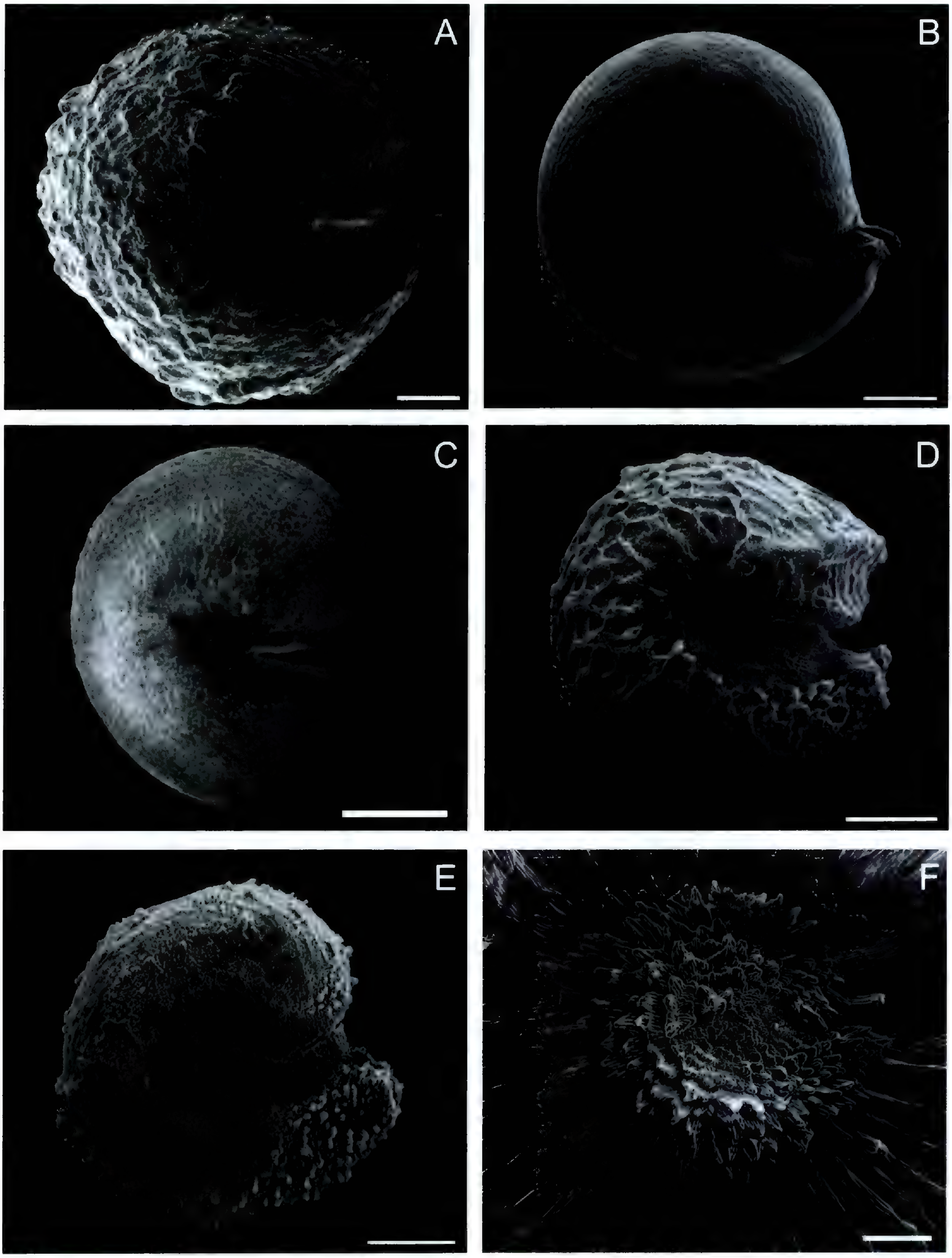


Figure 5. SEM micrographs of seed surfaces. —A. *Cleome anomala*. —B. *C. viridiflora*. —C. *C. chilensis*. —D. *C. chapalaensis*. —E. *C. psoraleaefolia*. —F. *C. stylosa*. Scale: A–F = 500 μm.

positioned on the back and claws of the seed (Iltis, 1952).

The cleft and cleft cavity of the seed also show much variation. In all taxa, the testa surrounds the entire seed surface, including the cleft cavity. The cleft can be open and very narrow (Fig. 4A), with a very small cleft cavity, as in *Cleome rutidosperma* (Fig. 6A), or short and mostly open (Figs. 4B, 5A, C), with the cleft cavity very narrow and very small, as in *C. lechleri* (Fig. 6B) and *Podandrogyne* (Fig. 6C). In the latter case, the membrane is deeply invaginated into the cleft, dividing it into two parts, with the mouth of the cleft open and with a small, internal, closed cleft cavity deep within the center of the seed. The cleft may be covered nearly its entire length by a thin membrane, as in *C. viridiflora* (Fig. 6D), where the cleft cavity is oblong and wide in longitudinal section. Sometimes the cleft is covered nearly its entire length by a hard membrane (Fig. 4C), with the cleft cavity itself very narrow in longitudinal section as in *Polanisia dodecandra* (Fig. 6F) and members of the North American group, or collapsed and essentially invisible, as in *C. sparsifolia* (Fig. 6E). Finally, in most members of section *Tarenaya*, the cleft membrane is either thin or thick, and covers three quarters or more of the cleft (Figs. 4D, F, 5D, E), so that the cleft cavity in longitudinal section is large and oblong (Fig. 7A, B) to obovoid (Fig. 7C, D) or spherical (Fig. 7E, F).

Pollen

The pollen of *Cleome* is tricolporate and highly variable in ornamentation, ranging from echinate to reticulate, rugulate, or verrucate-psilate. Typically, the entire pollen surface is ornamented, but in some species the ornamentation is restricted to the equatorial area. In *Cleome diffusa*, *C. werdermannii*, *C. chapalaensis*, and *C. aculeata* of section *Tarenaya* (Fig. 8A–D), *C. pilosa* of the Andean group, and *Podandrogyne macrophylla* (Fig. 8E, F) the whole surface is echinate. The surface of *C. rutidosperma* is rugulate-reticulate (Fig. 9A), and that of *C. gynandra*, *C. monophylla*, and *C. sparsifolia* is rugulate (Fig. 9B–D). The pollen surface of *C. anomala* (Fig. 10A), *C. moritziana* (Fig. 10B), and *C. lechleri* (Fig. 10C) of the Andean group and *C. stylosa* (Fig. 10D) to a lesser extent is echinate only in the equatorial region, and the remainder of the surface is psilate. That of *C. arborea* (Fig. 10E) and *C. viridiflora* (Fig. 10F) is mostly verrucate, but again psilate in the polar region.

Discussion

Phylogenetic Relationships

Maximum parsimony and maximum likelihood analyses support the monophyly of *Cleome* (including *Podandrogyne*), but with little bootstrap support (less than 50%). Within *Cleome*, there are three clades (Figs. 1–3). The African clade (77% bootstrap, 66% indels included) is composed entirely of Old World species, including the only member of section *Rutidosperma*, *Cleome rutidosperma*, a widespread African species and *C. monophylla*, another African species not previously assigned to a section. This clade is supported morphologically by having longitudinally striate and transversely ridged seed ornamentation (Fig. 4A, E), an open and very narrow seed cleft (Fig. 4A), with a very small, narrow cleft cavity just visible in longitudinal section (Fig. 6A), and rugulate or rugulate-reticulate ornamentation of the pollen (Fig. 9A, C). This last feature is similar to the outgroup *Polanisia dodecandra*, which differs only in having a more irregular (i.e., rugulate-heterobrocate) ornamentation (Fig. 9E).

The Andean plus Tarenaya clade, although only weakly supported (61% bootstrap indels included, Fig. 2), unites all the New World species of *Cleome* studied. Within the Tarenaya clade, *C. gynandra* of Africa, the only Old World species in the clade, is sister to *C. sparsifolia* of North America, but with weak support (65% and 69% indels included). Most of the South American species have bracteate inflorescences, although the strongly supported Ebracteate clade that includes *C. viridiflora*, *C. stylosa*, and *C. arborea* (100% bootstrap) lacks them.

The well-supported Andean clade (99% bootstrap) includes all species of the Andean group studied plus the two species of *Podandrogyne* studied. The woody, shrubby members of this clade grow at high elevations (1500–3800 m) in the Andes from Bolivia to Colombia and Venezuela, with one species in Mexico. The herbaceous annual *Cleome chilensis* grows mainly in desert areas along the coast, and its perennial sister in the mountains of northern Chile to central Peru, while the annual *C. pilosa* grows from Mexico and the West Indies to Ecuador and Venezuela at low to mid elevations. Morphologically, members of this clade have smooth (*C. chilensis*, Fig. 5C) to verrucose seeds (Figs. 4B, 5A). The open part of the seed cleft is short (Figs. 4B, 5A, C), because the membrane connecting the claws of the embryo is invaginated deeply within the cleft and is only visible in longitudinal section. Thus, the cleft cavity is also short and small (Fig. 6B, C).

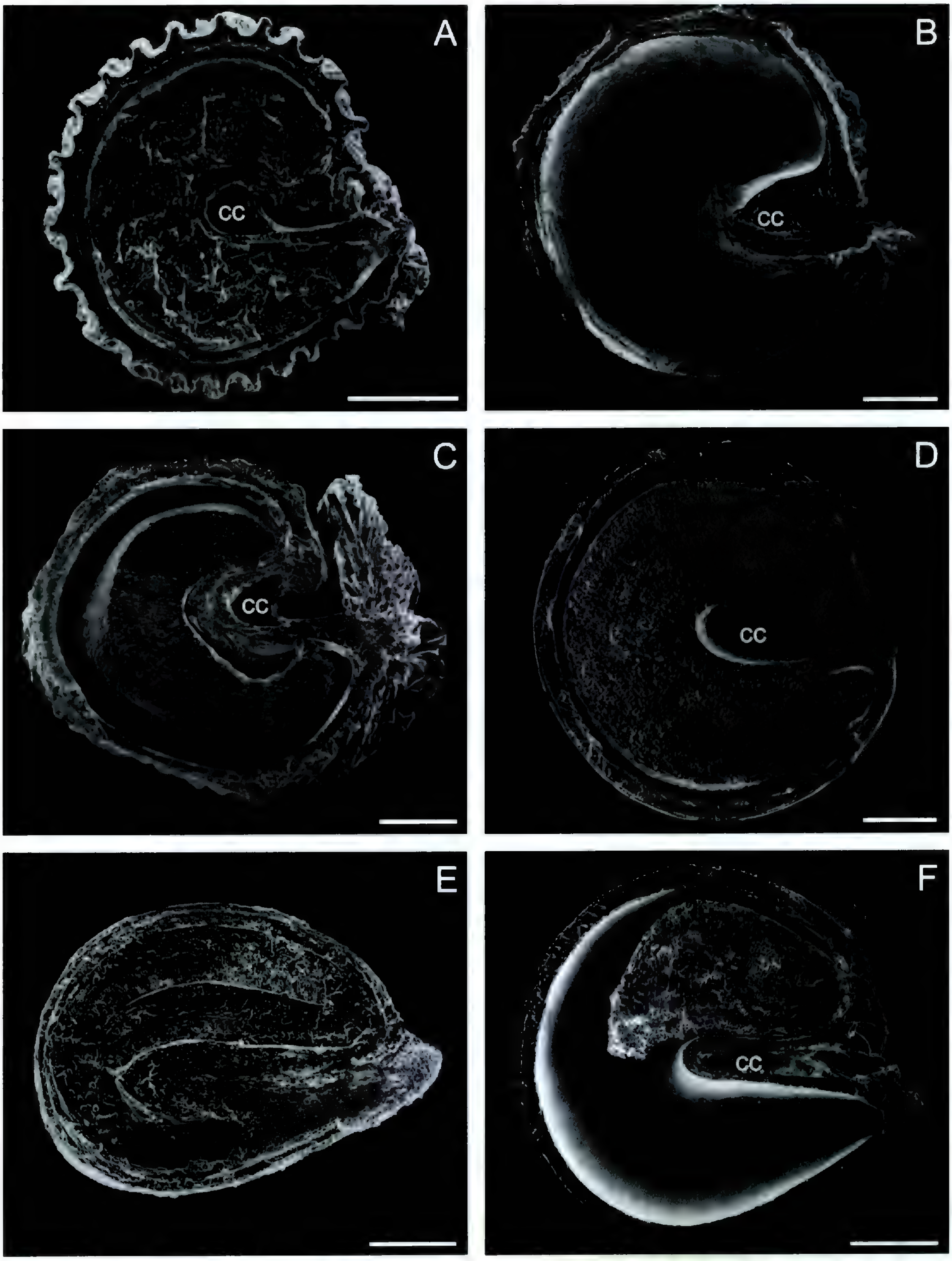


Figure 6. SEM micrographs of longitudinal sections of seeds showing the cleft cavity (cc). —A. *Cleome rutidosperma*. —B. *C. lechleri*. —C. *Podandrogyne macrophylla*. —D. *C. viridiflora*. —E. *C. sparsifolia* (no cleft cavity). —F. *Polanisia dodecandra*. Scale: A–F = 500 μm.

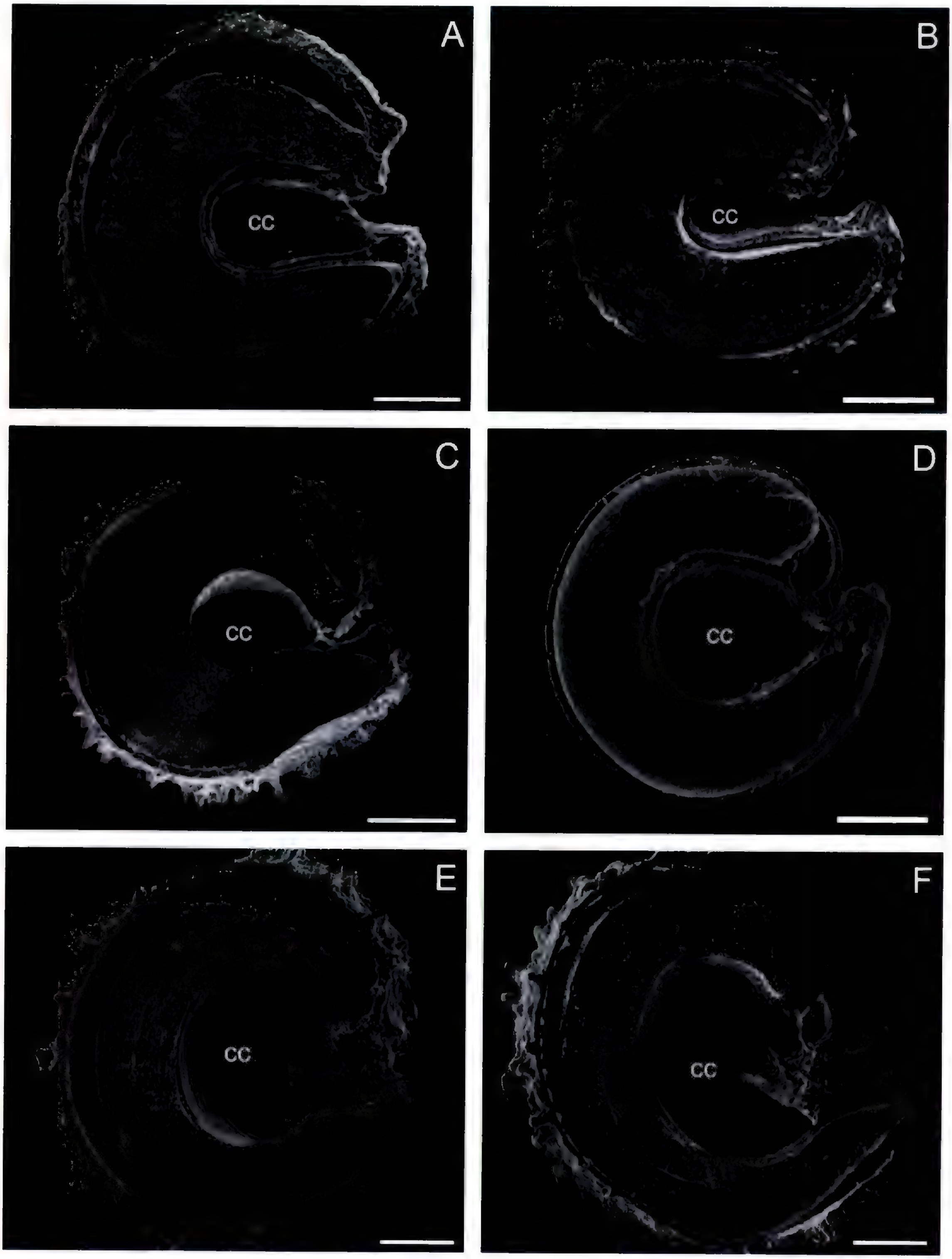


Figure 7. SEM micrographs of longitudinal sections of *Cleome* seeds showing the cleft cavity (cc). —A. *C. chapalaensis.* —B. *C. spinosa.* —C. *C. werdermannii.* —D. *C. brasiliensis.* —E. *C. cordobensis.* —F. *C. microcarpa.* Scale: A–F = 500 μm.

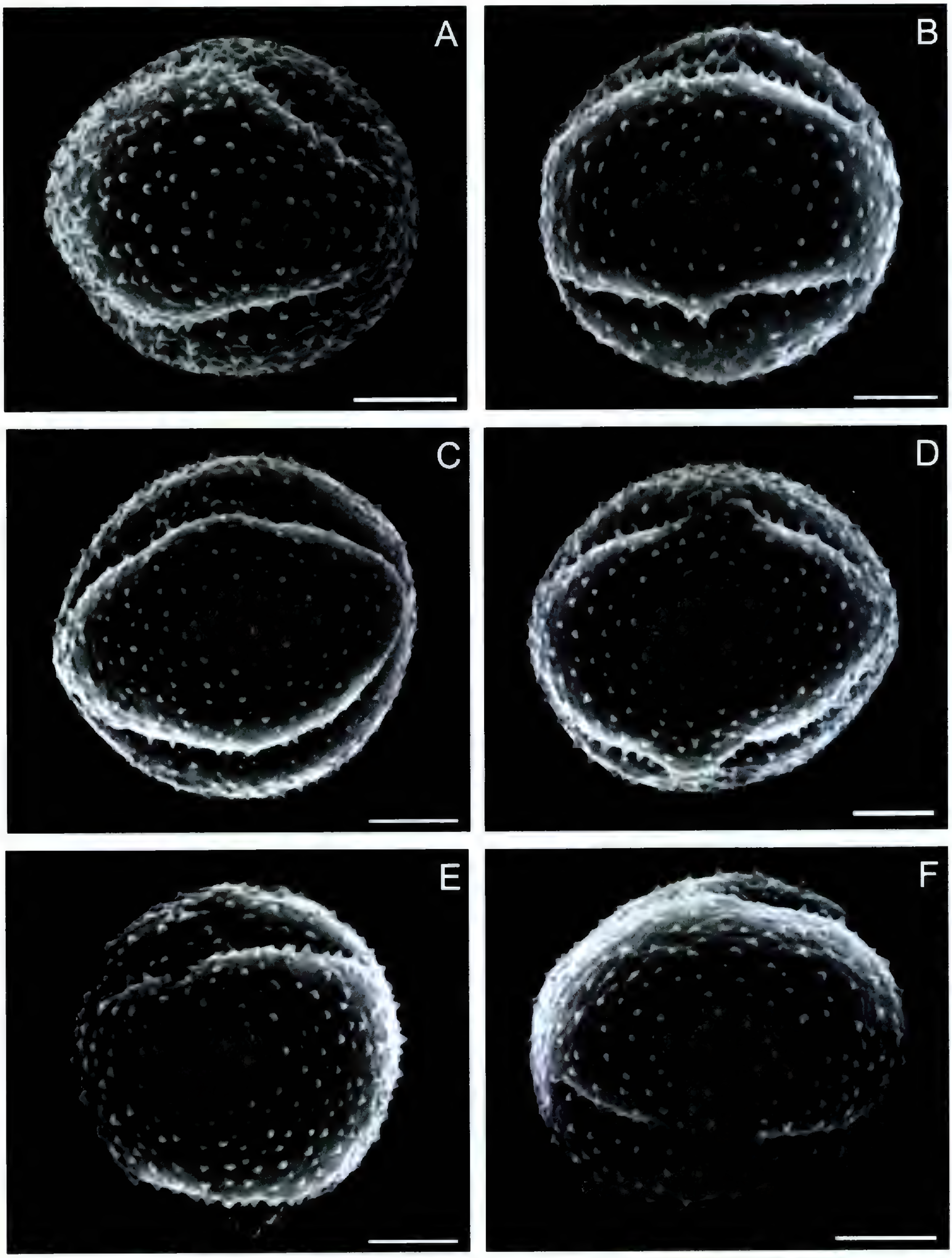
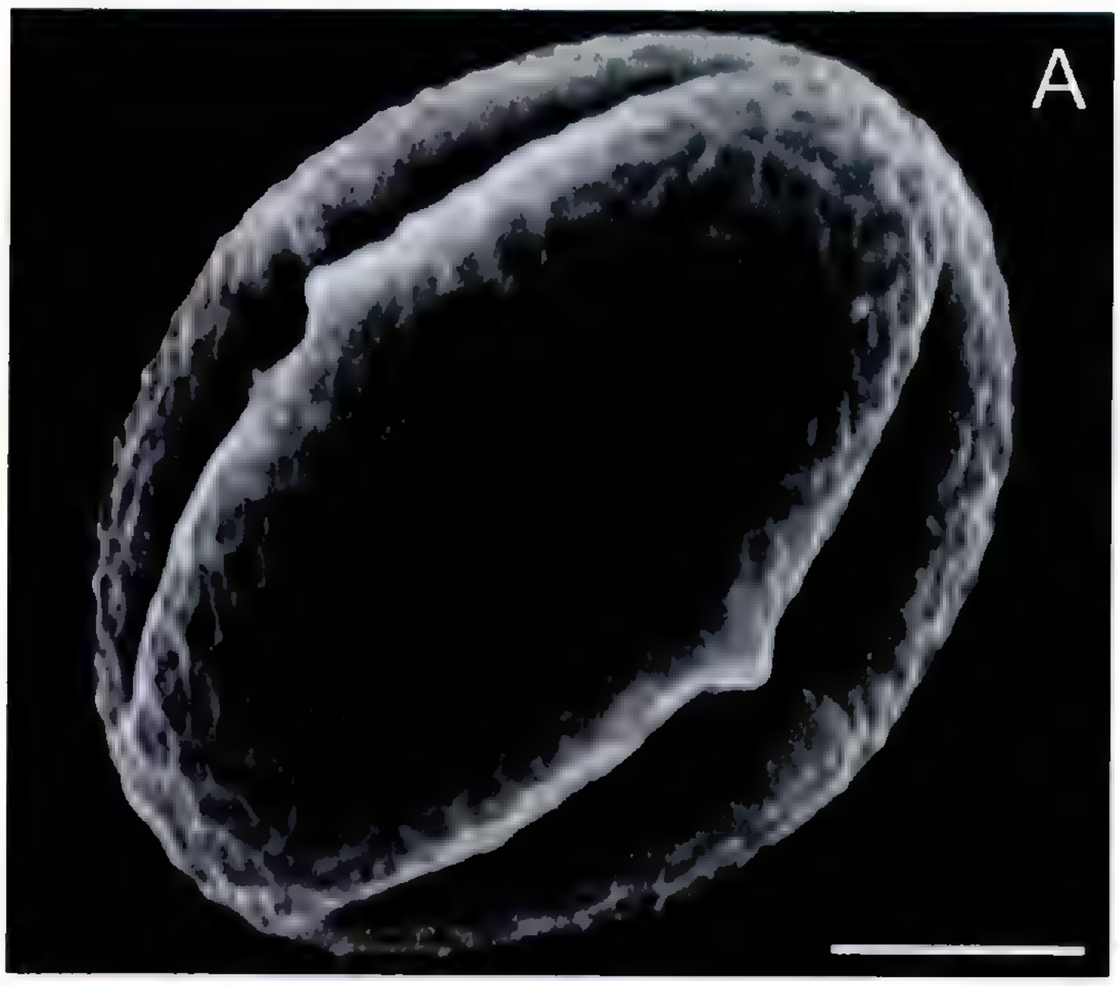
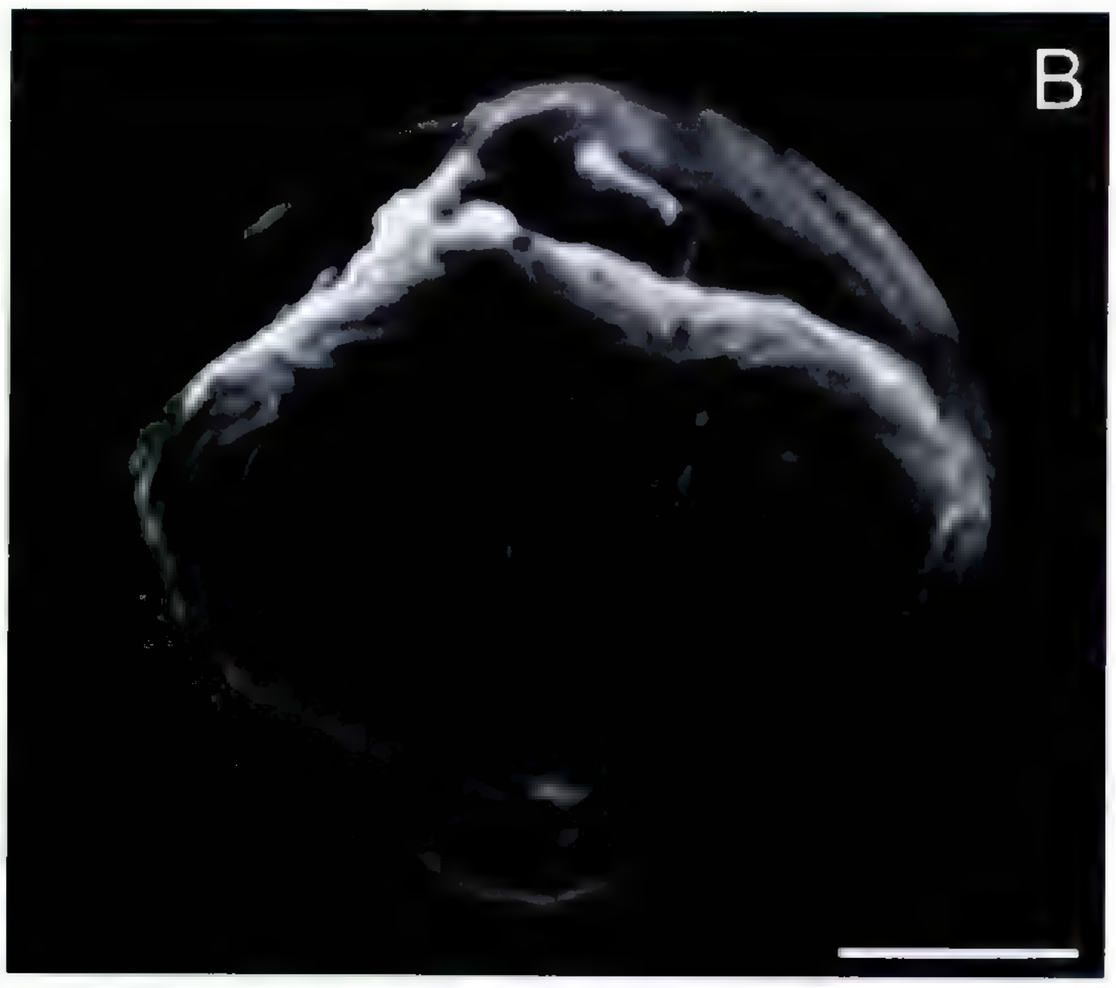
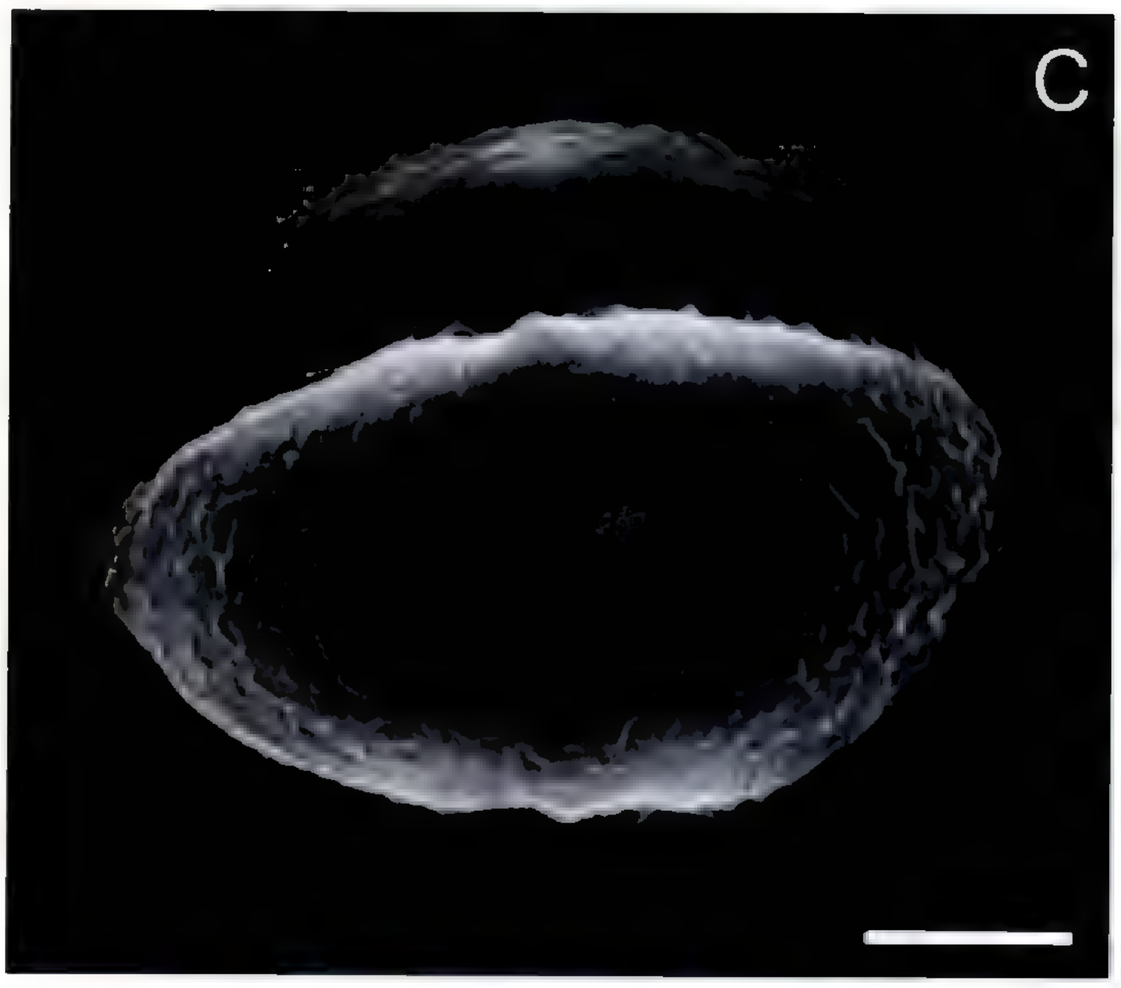
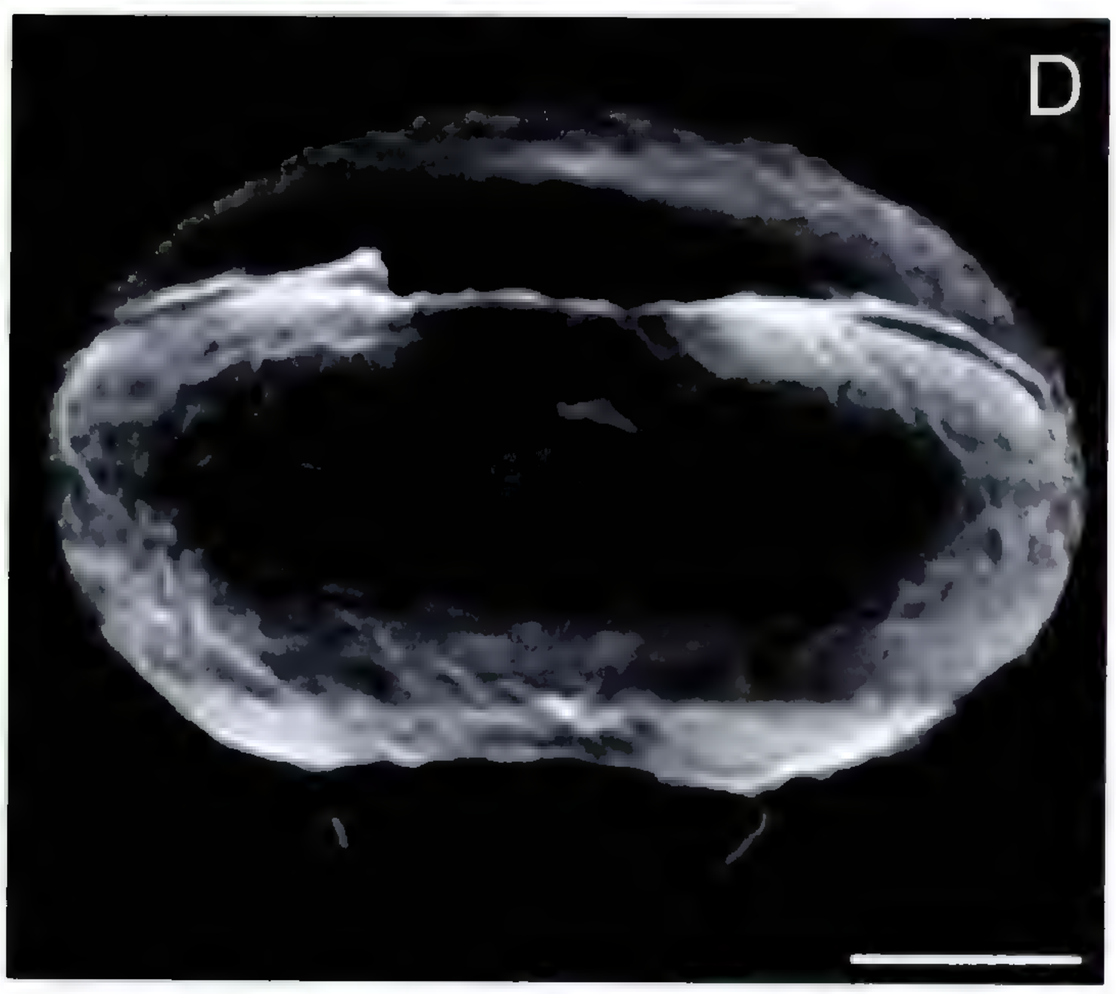


Figure 8. SEM micrographs of *Cleome* and *Podandrogyne* pollen in equatorial view. —A. *Cleome diffusa*. —B. *C. werdermannii*. —C. *C. chapalaensis*. —D. *C. aculeata*. —E. *C. pilosa*. —F. *Podandrogyne macrophylla*. Scale: A–F = 5 μm.









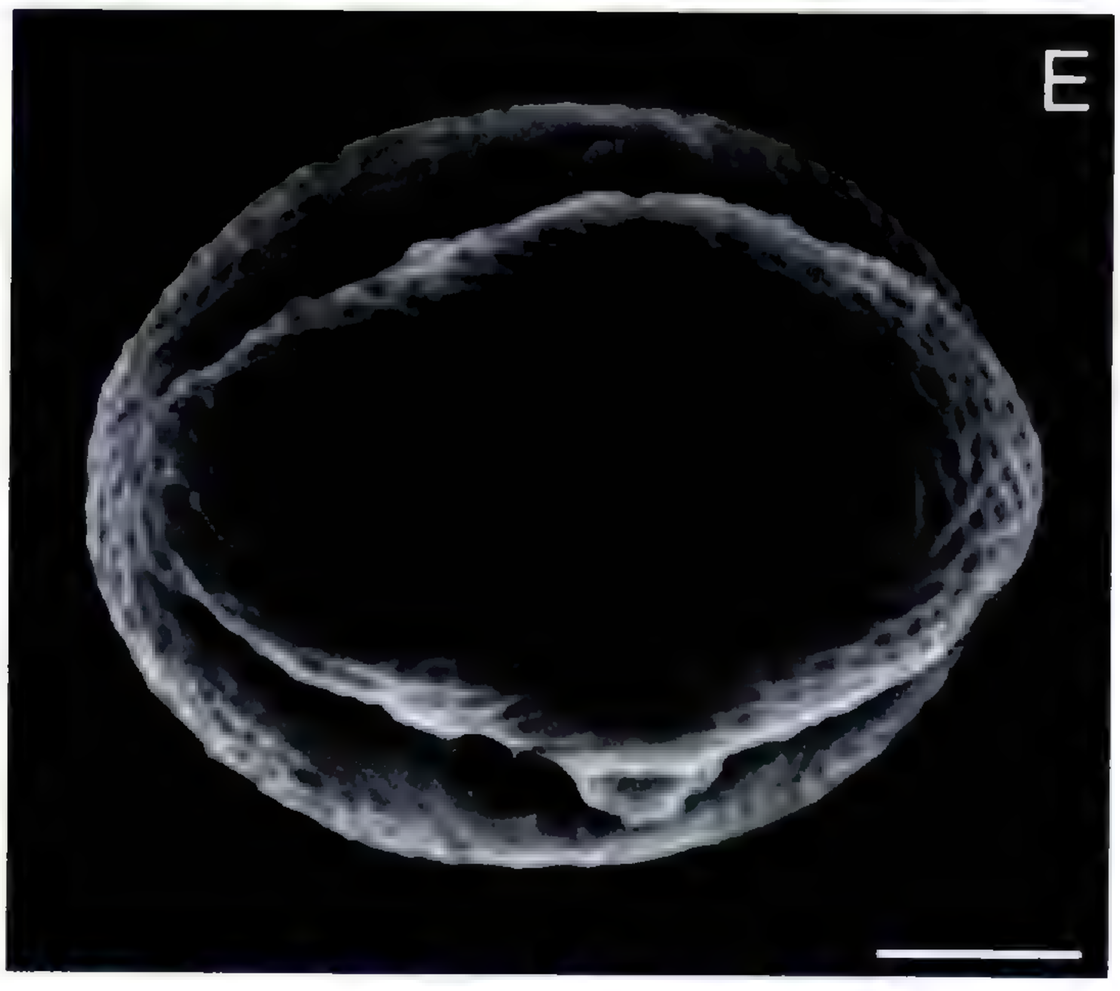


Figure 9. SEM micrographs of *Cleome* and *Polanisia* pollen in equatorial view. —A. *Cleome rutidosperma*. —B. *C. gynandra*. —C. *C. monophylla*. —D. *C. sparsifolia*. —E. *Polanisia dodecandra*. Scale: A–E = 5 μm.

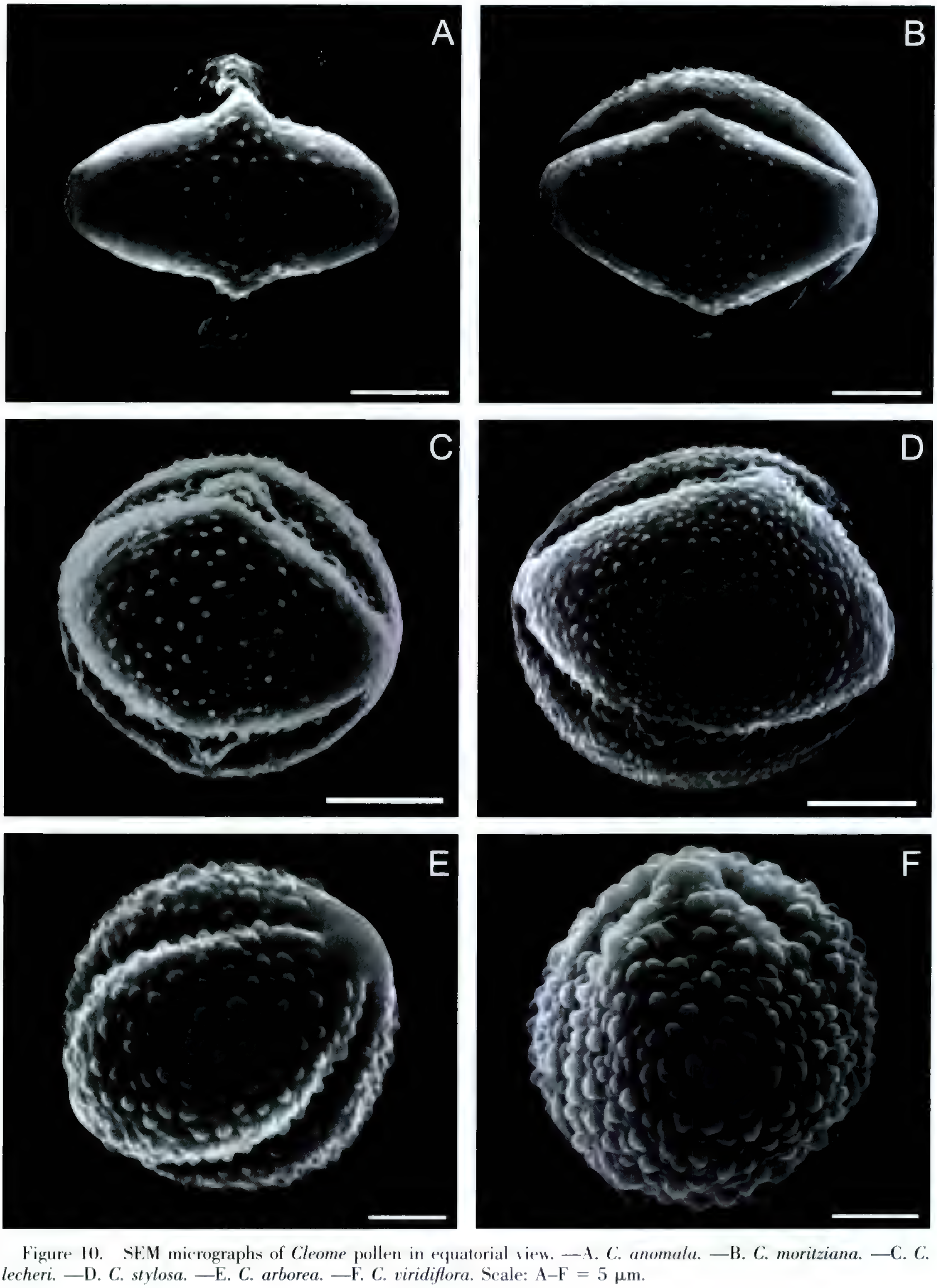


Figure 10. SEM micrographs of *Cleome* pollen in equatorial view. —A. *C. anomala.* —B. *C. moritziana.* —C. *C. lecheri.* —D. *C. stylosa.* —E. *C. arborea.* —F. *C. viridiflora.* Scale: A–F = 5 μm.

Within the Andean clade, there are two further well-supported clades. One of them includes the two species of *Podandrogyne* (100% bootstrap, 99% indels included) and *C. pilosa* (72% bootstrap, 68% indels included). This clade is also supported by the morphological synapomorphies of arillate seeds (Fig. 6C) and many-flowered, open racemes. A close relationship between *Podandrogyne* and members of the Andean group has been suggested previously (Cochrane, 1978; Iltis & Cochrane, 1989). However, *Podandrogyne* is generally segregated from *Cleome* (e.g., Mabberley, 1997) because of the presence of an androgynophore, monoecy, arillate seeds, and a peculiar fruit dehiscence (Iltis & Cochrane, 1989), in which, after the two fruit valves fall off, the two halves of the replum separate apically and twist a little, thereby exposing the seeds with their large white arils to ants, which act as dispersers. The second clade is formed by two woody shrubs, *Cleome anomala* and *C. moritziana* (94% bootstrap, 93% indels included). Both have prominently verrucose seeds (Fig. 5A) and, together with *C. lechleri*, usually have 5- to 9-foliolate leaves, a very dense and compact bracteate raceme, and flowers with thick, pubescent sepals. *Cleome chilensis*, on the other hand, is a highly modified desert annual. Iltis (1952) included it in the group of Andean species because the internal structure of its seeds is similar to other members of this subgenus. The results of the present study clearly support its inclusion in the Andean group.

Pollen in the Andean clade is quite variable. The two species of *Podandrogyne*, *Cleome pilosa*, and *C. chilensis* have echinate ornamentation over the entire surface of the pollen (Fig. 8E, F). The other three species (*C. anomala*, *C. moritziana*, and *C. lechleri*) have echinate ornamentation in the equatorial region, while a small to large area of the polar region is psilate (Fig. 10A–C). *Cleome moritziana* and *C. lechleri* have echinate ornamentation, with only a small polar area psilate (Fig. 10B, C). *Cleome anomala* has a rather narrow band of echinate ornamentation in the equatorial region, the rest of the grain being psilate (Fig. 10A). The study of Ruiz-Zapata and Xena de Enrech (1997: fig. 2a, c), documented similar ornamentation for *C. chilensis*, *C. anomala*, and *C. moritziana*.

The Tarenaya clade includes all species of section *Tarenaya* of Iltis (1952, 2005) plus *Cleome viridiflora* and *C. arborea* (Ebracteate group), *C. stylosa* (Winged group), *C. sparsifolia* (North American group), and *C. gynandra* of Africa (African sect. *Gymnogonia*). Although the Tarenaya clade has little bootstrap support (51% bootstrap, 64% indels included), most species also form a morphologically well-defined group. The seed cleft is closed for most of its length by a thin to thick membrane (Figs. 4D, F, 5B, D–F). The cleft cavity in the section is large and oblong (Figs. 6D, 7A, B), obovoid (Fig. 7C, D), or spherical (Fig. 7E, F). Furthermore, most species have echinate pollen (Fig. 8A–D) and most of the species have prickles on the stems that are especially large at the stipular position. However, the inclusion of *Cleome gynandra* of section *Gymnogonia* and *C. sparsifolia* of the North American group in this clade is not supported morphologically. The two species are supported as sister taxa (65% bootstrap, 69% indels included), and both have rugulate pollen (Fig. 9B, D). Furthermore, *C. sparsifolia* has the cleft closed along its entire length by a hard membrane (Fig. 4C), and no cleft cavity is visible even in cross section (Fig. 6E), while *C. gynandra* has an open cleft with a very small and narrow cleft cavity in cross section. Iltis (1952) suggested that *C. sparsifolia* is most likely a xerophytic derivative of section *Tarenaya*, in which, as an adaptation to desert conditions, the cleft became narrower and the membrane thicker, approaching the consistency of the testa. He also hypothesized that it could be related to some African groups.

Within the Tarenaya clade there are four well-supported clades (over 80% bootstrap) and three relatively well-supported clades (over 60% bootstrap, depending on whether or not indels are included). The first well-supported clade is the Spinosa clade (99% bootstrap, 100% indels included), which includes four species earlier grouped (subgroup E) by Iltis (1952). These species are sister to *Cleome chapalaensis* (53% bootstrap, 62% indels included), also placed in subgroup E by Iltis on morphological grounds. The Spinosa clade is characterized by the uniform presence of prickles in the stipular position, 5- to 7-foliolate leaves, large-flowered racemes, and a cleft cavity that appears oblong or obovoid to spherical in longitudinal sections of the seed (Fig. 7A–C). The second well-supported clade is the Parviflora clade, including *C. brasiliensis*, *C. parviflora*, and *C. psoraleaefolia* of subgroup E (Iltis, 1952). Iltis (1952) treated these three species as subspecies of *C. parviflora*. The Parviflora clade differs slightly from the Spinosa clade in having an obovoid to nearly spherical cleft cavity that is relatively large in longitudinal section (Fig. 7D). All members of the Spinosa and Parviflora clades have echinate ornamentation across the entire pollen surface (Fig. 8B), and the seed surface is smooth or scurfy (Fig. 5E).

A third clade (Arillate clade) with 84% bootstrap support (94% indels included) contains three close-

ly related species of subgroup C (*C. cordobensis*, *C. aculeata*, and *C. tucumanensis*). These species grow mainly in dry areas at relatively low elevations from sea level to 950 m. They have arillate seeds (Fig. 4F), with a very large, rounded cleft cavity (Fig. 7E) and a longitudinally striate, transversely ridged testa with hard excrescences that bear trichomes (Fig. 4F), and an echinate pollen surface (Fig. 8D). *Cleome microcarpa* and *C. diffusa*, the former in an unresolved position and the latter associated with *C. crenopetala*, although with only moderate support, also share these seed and pollen features. The seed morphology of *C. microcarpa* is similar to that of *C. diffusa* (Fig. 4D), both being cochleate-reniform. The seed cleft is wide, open at the mouth, and covered with a thin membrane that connects the tip of both ends of the embryo. The cleft cavity is essentially rounded, and the seeds have the same kind of white, spongy aril as the Arillate clade (Fig. 7F). *Cleome microcarpa*, a species of the dry caatinga has a distribution that overlaps somewhat in northeastern Brazil with the range of the coastal *C. diffusa*.

The two closely related species of the distinctive Ebracteate group (*C. viridiflora* and *C. arborea*) and the species of the Winged group (*C. stylosa*) form the fourth clade (100% bootstrap). These are similar only vegetatively and differ in seed and pollen morphology. The seeds of *C. viridiflora* and *C. arborea* (Ebracteate group) are smooth and varnished (Fig. 5B) and the cleft is closed along its entire length by a thin membrane (Fig. 5B), the cleft cavity being oblong (Fig. 6D). The seeds of *C. stylosa* (Winged group) are dramatically different, being winged and lamellate (Fig. 5F). The internal structure of the seed resembles more closely those of the Andean group, as stated by Iltis (1952). Pollen morphology also does not support this relationship. *Cleome viridiflora* and *C. arborea* have verrucate ornamentation (Fig. 10E, F), and *C. stylosa* (Fig. 10D) echinate ornamentation. Despite these differences, the analysis placed *C. viridiflora* sister to *C. stylosa* (65% bootstrap, 60% indels included). The three species grow in the Andes: *Cleome stylosa* is found in Venezuela and Colombia from 1500 to 2200 m, *C. viridiflora* has a broader distribution from Argentina to Mexico, and from sea level to 1800 m, while *C. arborea* is endemic to the coastal ranges of northern Venezuela.

Despite the great differences in seed and pollen morphology, the Arillate and Ebracteate clades are sister clades (89% bootstrap, 62% indels included) in the phylogentic analyses.

Also included within the Tarenaya clade is a small clade of two species, *Cleome paludosa* and *C. speciosa* (65% bootstrap indels included), both of which lack prickles and have minutely serrulate leaflets. The bracts in the inflorescence of *C. speciosa* are small, while the inflorescence in *C. paludosa* is ebracteate. The seeds are smooth to tuberculate, with small, superficial, scurfy excrescences. There is usually a large subspherical or obovoid cleft cavity similar to that of other species in subgroup E. A sister-group relationship between *C. crenopetala* and *C. diffusa* is also supported (72% bootstrap, 77% indels included). They typically have 3-foliolate leaves and grow in dry areas in eastern Brazil at relatively low elevations (0–800 m).

SYSTEMATIC IMPLICATIONS

Although there is little resolution of relationships among the deeper nodes of the phylogeny, this study does suggest that some of Iltis's (1952) sections are not monophyletic. For instance, the nesting of *Cleome stylosa* (Winged group) within the Ebracteate group (100% bootstrap), although not supported morphologically, makes the latter group paraphyletic. If the topology of the analysis that includes indels (Fig. 2) is confirmed, the subgroup E of section *Tarenaya* will be paraphyletic. Another notable result, which agrees with previous assertions by Hall et al. (2002) and Iltis and Cochrane (1989), is the inclusion of the genus *Podandrogyne* within the Andean clade (99% bootstrap support). The Andean clade, including *Podandrogyne*, is morphologically similar to the rest of the Neotropical *Cleome*, except in its internal seed structure. These results suggest that *Podandrogyne* should not be recognized as a separate genus.

CHARACTER EVOLUTION

The present study suggests that Old World species of *Cleome* are mostly basal to the New World species. This position is consistent with what is known of seed and pollen morphology. The Old World species tend to have the seed cleft open, but it may be so narrow as to appear closed (Fig. 4A), so that the cleft cavity in longitudinal section is small and very narrow (Fig. 6A). Thus *C. viscosa*, which appears to be closer to *Polanisia* than to *Cleome* s. str., also has the seed cleft open and narrow, while the cleft cavity in longitudinal section is practically absent. The Andean clade (Figs. 1, 2) is morphologically more closely related to the African clade (Old World species) in that they share a short open cleft that is cut off from the small internal cleft by a deep diagonal membrane (Figs. 4B, 5A, C), with the cleft cavity in section small

and narrow (Fig. 6B, C). Species of the Tarenaya clade (Fig. 1), on the other hand, have the cleft closed almost along its entire length (Figs. 4D, F, 5B, D–F), with the cleft cavity usually larger (Fig. 7C–F), although one group of species (*C. viridiflora, C. chapalaensis, C. spinosa*) has the cleft cavity smaller and oblong (Figs. 6D, 7A, B).

Pollen is also useful for grouping species of *Cleome*. The African species have reticulate (Fig. 9A) or rugulate pollen (Fig. 9B, C) similar to that of the outgroup *Polanisia*, which has rugulate-heterobrocate pollen (Fig. 9E). Species of section *Physostemon* (not included in this study), which grow in Mexico, the Caribbean, eastern Brazil, and Venezuela to Paraguay, also have reticulate pollen (Ruiz-Zapata & Xena de Enrech, 1997: fig. 4c, d), supporting the suggestion of Iltis (1952, 1959) that this section is more closely related to the Old World species. Indeed, in an analysis including all species (not shown), *Cleome stenophylla* and the Old World *C. gynandra*, both with incomplete sequences, were sister taxa. Members of the North American group have reticulate (Al-Shehbaz, 1973: plate 13, 1–4; plate 14, 1–8) or rugulate (Fig. 9D) pollen ornamentation. Pollen morphology and the placement of *C. sparsifolia* (North America) and *C. gynandra* (Africa) as sister species suggest that these species may also be closely related to the African species. All members of section *Tarenaya* (Fig. 8A–D) plus some members of the Andean group (Fig. 8E, F) and the two species of *Podandrogyne* (Fig. 8F) are echinate over the entire surface. This suggests that echinate pollen may be derived from reticulate or rugulate pollen, contrary to the suggestion of Ruiz-Zapata and Xena de Enrech (1997). However, while *C. arborea* (Fig. 10E) and *C. viridiflora* (Fig. 10F) have verrucate ornamentation, *C. stylosa* (Fig. 10D) has echinate ornamentation, very similar to that of *C. lechleri* (Fig. 10C). The sister species *C. anomala* and *C. moritziana* (Fig. 10A, B) have echinate ornamentation in the equatorial region, with the rest of the pollen surface psilate.

The phylogenetic results presented in this study help to clarify several aspects of morphological evolution within *Cleome*. For example, the results do not support Iltis's (1952) suggestion that his South American section *Tarenaya* is the most primitive of the New World species groups because of its putatively primitive seed structure (big, rounded seed cavity) and its distribution in the ancient east Brazilian landmass. On the other hand, Iltis's prediction that the presence of an aril, prickles, and a large cleft cavity in the seed are derived characters is supported by the phylogenetic data. Future phylogenetic work on *Cleome* should increase taxon sampling and explore additional gene regions; in particular, the focus must shift to the Old World species.

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Appendix 1. List of sequences analyzed and herbarium vouchers of the species studied.

Species	GenBank #	Voucher #		
		DNA	Pollen	Seed
C. aculeata L.	AJ876563	Bolivia. Santa Cruz: *Sánchez et al. 1117* (USZ)	Bolivia. Santa Cruz: *Sánchez et al. 1117* (USZ)	Bolivia. Santa Cruz: *Sánchez et al. 1117* (USZ)
C. anomala HBK	AJ786564	Venezuela. Táchira: *Ruiz & Hernández 4980* (MY)	Ecuador. Tungurahua: *Asplund 8111* (MO)	Ecuador. Imbabura: *Peñafiel & Tamayo 267* (MO)
C. arborea HBK	AJ876565	Venezuela. Mérida: *Catalán 98* (MERC)	Venezuela. Mérida: *Ruiz & Hernández 4981* (MY)	Venezuela. *Fendler 28* (MO)
C. boliviensis Iltis	n/a	Bolivia. Santa Cruz: *Sánchez et al. 1116* (USZ)	Bolivia. Santa Cruz: *Sánchez et al. 1116* (USZ)	Bolivia. Santa Cruz: *Sánchez et al. 1116* (USZ)
C. brasiliensis Weinm.	AJ876566	Bolivia. Beni: *Guareco 539* (LPB)	Bolivia. Cochabamba: *Steinback 378* (MO)	Brazil. Sta. Catarina: *Rambo 31593* (MO)
C. chapalaensis Iltis	AJ876567	Mexico. Michoacán: *Iltis et al. 832* (USZ)	Mexico. Michoacán: *Iltis et al. 832* (USZ)	Mexico. Michoacán: *Iltis et al. 832* (USZ)
C. chilensis DC.	AJ876568	Peru. Piura: *Croat 58408* (MO)	Peru. Piura: *Croat 58408* (MO)	Chile. Antofagasta: *Taylor et al. 10727* (MO)
C. cordobensis Eichler ex Griseb.	AJ876569	Bolivia. Tarija: *Ehrich 8* (LPB)	Bolivia. Santa Cruz: *Nee 33569* (USZ)	Bolivia. Tarija: *Bastián 382* (LPB)
C. crenopetala DC.	AJ876570	Brazil. Paraná: *Dusén 7365* (MO)	Brazil. Paraná: *Dusén 7365* (MO)	
C. dendroidea Schult. f.	n/a	Brazil. Rio de Janeiro: *Maas 3159* (MO)	Brazil. Rio de Janeiro: *Maas 3159* (MO)	Brazil. Rio de Janeiro: *Corcovado 4139* (MO)
C. diffusa Banks ex DC.	AJ876571	Brazil. Bahía: *Harley et al. 17276* (MO)	Brazil. Bahía: *Harley et al. 17276* (MO)	Brazil. Bahía: *Harley et al. 17276* (MO)
C. gynandra L. (Africa)	AJ876572	Southern Africa. Klerksdorp, W. Transvaal, *Bayliss 3879* (MO)	Southern Africa. Klerksdorp, W. Transvaal, *Bayliss 3879* (MO)	Southern Africa. Great Namagualand, *Ortendahl 463* (MO)
C. gynandra L. (South America)	n/a	Venezuela. Trujillo: *Ruiz & Villafañe 4990* (MY)	Venezuela. Aragua: *Ruiz & Hernández 4974* (MY)	Colombia. Magdalena: *Romero-Castañeda 10779* (MO)
C. hassleriana Chod.	AJ876573	U.S.A. Mississippi: *MacDonald et al. s.n.* (MO)	Brazil. Caxias do Sul: *Grazziotin & Peruffo 3721* (MO)	Paraguay. Caaguazú: *Fernandez-Casas & Molero 4247* (MO)
C. lechleri Eichler	AJ876574	Bolivia. La Paz: *Sánchez et al. 1129* (USZ)	Bolivia. La Paz: *Sánchez et al. 1129* (USZ)	Bolivia. La Paz: *Sánchez et al. 1133* (USZ)
C. microcarpa Ule	AJ876575	Brazil. Bahía: *Harley 27228* (MO)	Brazil. Bahía: *Harley 27228* (MO)	Brazil. Bahía: *Harley 16861* (MO)
C. monophylla L.	AJ876576	Senegal. Réserve de Bondia, *Dniort 42* (MO)	Ethiopia. Shoa Region, *Gilbert & Thulin 213* (MO)	Senegal. Réserve de Bondia, *Dniort 42* (MO)
C. moritziana Klotzch ex Eichler	AJ876577	Venezuela. Mérida: *Rodríguez & Catalán 97* (MERC)	Venezuela. Aragua: *Steyermark & Liesner 121991* (MO)	Colombia. Guajira: *Cuadros & Gentry 3508* (MO)
C. paludosa Eichler	AJ876578	Bolivia. Santa Cruz: *Guillén et al. 5344* (USZ)	Bolivia. Santa Cruz: *Nee 48431* (MO)	Bolivia. Santa Cruz: *Nee 48431* (MO)
C. parviflora HBK	AJ876579	Bolivia. Santa Cruz: *Sánchez et al. 1135* (USZ)	Bolivia. Beni: *Foster 12516* (LPB)	Bolivia. Pando: *Nee 31769* (LPB)
C. psoraleaefolia DC.	AJ876580	Bolivia. Santa Cruz: *Seidel 132* (USZ)	Bolivia. Santa Cruz: *Seidel 132* (USZ)	Bolivia. Beni: *Nee 37166* (LPB)
C. pilosa Benth.	AJ876581	Venezuela. Aragua: *Ruiz & Hernández 5012* (MY)	Peru. Tumbes: *Díaz et al. 4759* (MO)	Peru Tumbes: *Díaz et al. 4759* (MO)
C. rosea Vahl ex DC.	AJ876582	Brazil. Pernambuco: *Costa & Silva 1530* (MO)	Brazil. Pernambuco: *Costa & Silva 1530* (MO)	

Appendix 1. Continued.

Species	GenBank #	Voucher #		
		DNA	Pollen	Seed
C. sp. nov. affinis *pernambucensis*	n/a	Brazil. Pernambuco: *Costa & Silva 1529* (MO)	Brazil. Pernambuco: *Costa & Silva 1529* (MO)	Brazil. Pernambuco: *Costa & Silva 1529* (MO)
C. rutidosperma DC. (Africa)	AJ876583	Cameroon. *Thompson & Rawlins 1498* (MO)	Central African Republic. Sangha, *Harris & Fay 308* (MO)	Cameroon. *Thompson & Rawlins 1498* (MO)
C. rutidosperma DC. (South America)	AJ876584	French Guiana. Cayenne, *Torke 217* (MO)	French Guiana. Cayenne, *Torke 217* (MO)	French Guiana. Cayenne, *Torke 217* (MO)
C. sparsifolia S. Watson	AJ876585	U.S.A. Nevada: *Williams & Tiehm 82491* (MO)	U.S.A. Nevada: *Williams & Tiehm 82491* (MO)	U.S.A. California: *Walker 3494* (MO)
C. speciosa Raf.	AJ876586	Venezuela. Táchira: *Ruiz & Hernández 4978* (MY)	Venezuela. Táchira: *Ruiz & Hernández 4978* (MY)	Colombia. Putumayo: *Klug 1660* (MO)
C. spinosa Jacq.	AJ876587	Brazil. Pernambuco: *Costa & Silva 1522* (MO)	Brazil. Pernambuco: *Costa & Silva 1522* (MO)	Brazil. Pernambuco: *Costa & Silva 1522* (MO)
C. stenophylla Klotzch ex Urb.	n/a	Venezuela. Guárico: *Ruiz & Villafañe 4971* (MY)	Venezuela. Guárico: *Ruiz & Villafañe 4971* (MY)	Nicaragua. Granada: *Stevens 4604* (MO)
C. stylosa Eichler	AJ876588	Venezuela. Táchira: *Ruiz & Hernández 4977* (MY)	Venezuela. Táchira: *Ruiz & Hernández 4977* (MY)	Colombia. Chocó: *Gentry & Renteria 23699* (MO)
C. titubans Speg.	AJ876589	Argentina. Buenos Aires: *Krapovickas 2897* (MO)	Argentina. Buenos Aires: *Krapovickas 2897* (MO)	Argentina. Buenos Aires: *Krapovickas 2897* (MO)
C. tucumanensis Iltis	AJ876590	Bolivia. Santa Cruz: *Sánchez et al. 1114* (USZ)	Bolivia. Santa Cruz: *Sánchez et al. 1114* (USZ)	Bolivia. Santa Cruz: *Sánchez et al. 1114* (USZ)
C. viridiflora Schreb.	AJ876591	Venezuela. Aragua: *Ruiz 5010* (MY)	Bolivia. Cochabamba: *Maas et al. 8803* (LPB)	Bolivia. Santa Cruz: *Menacho 675* (USZ)
C. viscosa L.	AJ876592	Venezuela. Portuguesa: *Ruiz & Villafañe 4963* (MY)	Nicaragua. Carazo: *Stevens et al. 2705* (MO)	Mexico. Campeche: *Cabrera 14796* (MO)
C. werdermannii A. Ernst	AJ876593	Bolivia. Santa Cruz: *Sánchez et al. 1111* (USZ)	Bolivia. Santa Cruz: *Sánchez et al. 1111* (USZ)	Bolivia. Santa Cruz: *Sánchez et al. 1111* (USZ)
Podandrogyne brachycarpa (DC.) Woodson	AJ876594	Ecuador. Pastaza: *Croat 72841* (MO)	Ecuador. Napo: *Cerón & Hurtado 6571* (MO)	Ecuador. Morona-Santiago: *Espinoza & Castañel 779* (MO)
Podandrogyne macrophylla (Turcz.) Woodson	AJ876595	Venezuela. Mérida: *Ruiz & Hernández 4982* (MY)	Venezuela. Mérida: *Hahn & Grifo 3315* (MO)	Venezuela. Mérida: *Hahn & Grifo 3315* (MO)
Polanisia dodecandra (L.) DC.	AJ876596	U.S.A. Missouri: *Stevens s.n.* (MO)	U.S.A. Missouri: *Stevens s.n.* (MO)	U.S.A. Missouri: *Stevens s.n.* (MO)

PHYLOGENY AND GEOGRAPHY OF *SCHEFFLERA*: PERVASIVE POLYPHYLY IN THE LARGEST GENUS OF ARALIACEAE[1]

Gregory M. Plunkett,[2] Porter P. Lowry II,[3] David G. Frodin,[4] and Jun Wen[5]

Abstract

The angiosperm family Araliaceae presently comprises roughly 1600 species, over half of which are referable to a single genus, *Schefflera*, whose circumscription has been broadened substantially over the past three decades. Following up on several previous analyses suggesting that *Schefflera* may be non-monophyletic, the present study employs an expanded sample of species from this genus, representing much more of the geographic and taxonomic breadth of *Schefflera* in its current circumscription. Results of phylogenetic analyses based on nuclear (ITS) and plastid (*trn*L-*trn*F) DNA sequences indicate that *Schefflera* is markedly polyphyletic, comprising no fewer than five major clades distributed across the phylogenetic tree of Araliaceae. However, despite its overall polyphyly, the reinstatement of most formerly recognized segregate genera would not yield monophyletic groups. By contrast, comparisons of the molecular cladograms to an informal classification system based on morphology indicate that all but one of its infrageneric groupings are monophyletic. The five clades of *Schefflera* recognized here also correspond perfectly to geographic distributions: two morphologically distinct clades are centered in the southwest Pacific, and three other clades are centered in the Neotropics, Asia/Malesia, and Africa/Madagascar.

Key words: Araliaceae, ITS, phylogeny, polyphyly, *Schefflera*, *trn*L-*trn*F.

Much recent progress has been made in understanding the phylogeny of the family Araliaceae, including its circumscription, its historically troublesome relationship to Apiaceae (and other elements in the order Apiales), and relationships among its roughly 41 genera (e.g., Plunkett et al., 1996, 1997, 2004a, c; Plunkett, 2001; Plunkett & Lowry, 2001; Lowry et al., 2001, 2004; Wen et al., 2001). Additional studies have examined relationships within and among several genera (or generic groups) in the family, including *Aralia*, *Brassaiopsis*, *Hedera*, *Meryta*, *Panax*, *Polyscias*, *Pseudopanax*, *Raukaua*, and *Tetraplasandra*, inter alia (Wen & Zimmer, 1996; Wen & Nowicke, 1999; Mitchell & Wagstaff, 1997; Wen, 2001b; Costello & Motley, 2001; Eibl et al., 2001; Plunkett et al., 2001; Ackerfield & Wen, 2002, 2003; Valcárcel et al., 2003; Mitchell & Wen, 2004; Plunkett et al., 2004b; Tronchet et al., in press). Yet, of the roughly 1600 species of Araliaceae, over half belong to a single genus, *Schefflera* J. R. Forst. & G. Forst. Earlier studies have contributed to the description of infrageneric groups within *Schefflera* (Frodin, 1975, 1986, 1989, 1993, 1995), but huge gaps remain in our understanding of this complex genus. Even now, over a third of its estimated 900 species await formal description. Moreover, apart from the inclusion of a modest number of species in family-wide

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[2] Department of Biology, Virginia Commonwealth University, P.O. Box 842012, Richmond, Virginia 23284-2012, U.S.A. gmplunke@vcu.edu.

[3] Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A.; and Département Systématique et Evolution, Muséum National d'Histoire Naturelle, Case Postale 39, 57 rue Cuvier, 75231 Paris CEDEX 05, France.

[4] Chelsea Physic Garden, 66 Royal Hospital Road, London SW3 4HS, United Kingdom; and Royal Botanic Gardens, Kew, Richmond, Surrey TW9 3AE, United Kingdom.

[5] Department of Botany, Field Museum of Natural History, Chicago, Illinois, U.S.A.; Laboratory of Systematic and Evolutionary Botany, Institute of Botany, the Chinese Academy of Sciences, Beijing 100093, China; current address: Department of Botany, National Museum of Natural History, MRC-166, Smithsonian Institution, P.O. Box 37012, Washington, D.C. 20013-7012, U.S.A.

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studies of Araliaceae (Wen et al., 2001; Plunkett et al., 2001, 2004c), almost no work has been undertaken to evaluate *Schefflera* as a whole from a phylogenetic perspective. Nonetheless, these broad studies have shown that *Schefflera* may be polyphyletic. Given the importance of *Schefflera* to the understanding of classification and phylogeny in Araliaceae, a series of long-term studies of the entire genus has been initiated. The present analysis represents our first effort toward elucidating relationships among the major groups of *Schefflera*.

Schefflera is typified by the New Zealand species *S. digitata* J. R. Forst. & G. Forst., which was described soon after the return of James Cook from his second voyage of exploration (Forster & Forster, 1775). During the next ca. 75 years, *Schefflera* remained narrowly circumscribed to include only *S. digitata* and a second species from nearby Fiji (*S. vitiensis*), while nearly 100 additional species described during this period (and now placed in *Schefflera*) were referred to other genera, including *Heptapleurum* Gaertn. (36 species, Asia and Malesia) and *Sciodaphyllum* (24 species, Americas and Africa). This trend persisted through the 1860s, as reflected in the family-level treatments of Seemann (1868) and Bentham (1867). Adoption of a substantially broader circumscription of *Schefflera* was originally proposed by Baillon (1878, 1879) and subsequently embraced by Harms (1894–1897) and Viguier (1906, 1909). These authors had access to a rapidly growing number of new discoveries (including many from New Caledonia and the fringes of highland Guyana) that, combined with their more synthetic view of relationships, prompted them to question earlier generic distinctions. Harms in particular circumscribed *Schefflera* to include all araliads with a woody habit (trees, shrubs, epiphytes, hemiepiphytes, or climbers), once palmately compound leaves, stipules fused into ligular appendages, and inflorescences of compound umbels or panicles (of umbellules, capitula, racemules, or spicules), but lacking both articulated pedicels and armed structures on vegetative organs (see Frodin, 1975). Harms maintained a few distinct genera characterized primarily by bi- or pluricarpellate ovaries (and anisomery of carpels and stamens), such as *Didymopanax* and *Plerandra*, and also recognized *Dizygotheca* based on its unusual anther morphology. Notwithstanding these segregates, however, this broadly defined interpretation of *Schefflera* has been adopted almost unanimously for nearly a century and a half. As such, the genus is by far the largest in Araliaceae, but it was not until the 1970s that its current size was fully appreciated. In spite of the many new species described in the first two-thirds of the 20th century, modest estimates of only ca. 150 to 200 species were commonly cited (e.g., Dalla Torre & Harms, 1900–1907: 363; Willis, 1931; Melchior, 1964: 371; Willis, 1966, 1973). Even Hutchinson (1967), in the first serious survey of the family since those of Harms and Viguier, indicated a mere 125 species for *Schefflera*, and only about 60 more in several of his segregates, such as the racemosely flowered species of *Agalma* and the aggregate-fruited *Brassaia*. Shortly thereafter, however, Frodin (1975: 435) further enlarged *Schefflera* to include all woody araliads with palmately compound leaves, ligulate stipules and valvate aestivation, but without armament or articulated pedicels in the flowers. Based on a worldwide species-level reassessment, he estimated that the genus comprised ca. 450 species. Continued field and herbarium research during the last three decades has now increased the number of described species to 582 (Frodin & Govaerts, 2003) with, as noted above, at least 300 more still to be described.

Schefflera thus now includes species that have, at one time or another, been referred to 12 additional segregate genera, viz. *Agalma*, *Brassaia*, *Crepinella*, *Didymopanax*, *Dizygotheca*, *Geopanax*, *Heptapleurum*, *Octotheca*, *Plerandra*, *Schefflerop sis*, *Sciadophyllum*, and *Tupidanthus*. A few of these segregates, particularly *Didymopanax*, *Dizygotheca*, *Plerandra*, and *Tupidanthus*, were widely accepted until the latter part of the 20th century. Regardless of whether the segregate genera are maintained, however, *Schefflera* dwarfs all other genera in the family, including *Polyscias*, with ca. 150 species (Plunkett et al., 2001, 2004b, c; Lowry et al., 2004), *Oreopanax* with 148 species, *Dendropanax* with 92, and *Aralia* with 67 (Frodin & Govaerts, 2003).

Within *Schefflera*, Harms (1894–1897) was the first author to propose an infrageneric classification scheme, followed by Viguier (1909) and much later Bernardi (1979). Harms created two sections, sect. *Cephaloschefflera* (for species with flowers in heads) and sect. *Euschefflera* (for those with pedicellate flowers). Within section *Euschefflera* he recognized a number of smaller unranked (and partially unnamed) subgroups. A third section was added later to accommodate *S. diplodactyla* Harms (Harms, 1940: 52). Viguier (1909) adopted a somewhat different system, using "synoptic keys," but his infrageneric groups were not given formal rank. Local and regional treatments have also been published that recognize infrageneric groups, the earliest by Blume (1825–1827) and more recently by Hoo and Tseng (1965) and Shang (1984) for China and

southeast Asia, Smith and Stone (1968) and Smith (1985) for the south-central Pacific (and Fiji), Bernardi (1969) for Madagascar, Maguire et al. (1984) for the Guyana Highlands, Lowry (1989) for Vanuatu, and Frodin (1993) for northern South America. Other indications of infrageneric groups or relationships among species have been provided in studies by Frodin (1975, 1986, 1989, 1995) and Lowry et al. (1989), but as yet no modern comprehensive infrageneric classification has been published.

An unpublished and informal infrageneric system has, however, been developed by the third author, which we summarize in Table 1. Ten subgeneric groups are recognized on the basis of morphology, most of which are further subdivided into informal infrageneric groups. Nearly all of Frodin's groups correspond closely to geographic distribution. Two groups are centered in southeast Asia ("Agalma" from Asia and Malesia, and "Parapanax" from Malesia), four in the New World ("Cephalopanax" and "Cotylanthes" in Andean South America and Panama, "Crepinella" from northern South America, and "Didymopanax" more broadly distributed in northern, eastern, and middle South America, but best represented in Brazil), two in the southwest Pacific Ocean basin ("Plerandra" and "Schefflera"), one in tropical Africa and Madagascar ("Meiopanax"), and one more broadly distributed ("Sciodaphyllum," from Central and South America, Africa, Malesia, and Asia). These informal subgeneric groups represent working hypotheses that can be used to test and evaluate relationships among the species currently included in *Schefflera*.

Given the indications from previous studies that the current, broad circumscription of *Schefflera* may comprise a polyphyletic group (Plunkett et al., 2001, 2004c; Wen et al., 2001), we have employed molecular data to evaluate the probable non-monophyly of this genus and to test the basic framework of Frodin's (unpublished) infrageneric groups (Table 1). While many recent studies have demonstrated the utility of molecular data for phylogenetic analysis in Araliaceae, some markers have proved too conservative to be used at intergeneric and interspecific levels in this family. Among these are the plastid genes *rbc*L and *mat*K—now demonstrated to be better suited to familial and interfamilial levels in Apiales (e.g., Plunkett et al., 1996, 1997; Plunkett & Lowry, 2001). By contrast, the internal transcribed spacers (ITS) of nuclear rDNA have been useful at several taxonomic levels in Araliaceae, including within and among closely related genera (e.g., *Aralia*, *Brassaiopsis*, *Meryta*, *Panax*, *Polyscias*, *Pseudopanax*, and *Tetraplasandra*; see Costello & Motley, 2001; Mitchell & Wagstaff, 1997; Mitchell & Wen, 2004; Plunkett et al., 2001, 2004b; Wen & Zimmer, 1996; Wen et al., 2003; Tronchet et al., in press), and for intergeneric relationships across the family as a whole (Lowry et al., 2004; Plunkett et al., 2004c; Wen et al., 2001). To clarify relationships suggested by phylogenetic analysis of ITS data, several studies have recently used sequences from the *trn*L-*trn*F region (including the *trn*L intron and the *trn*L-*trn*F intergenic spacer) of the chloroplast genome both at interspecific (e.g., Eibl et al., 2001; Plunkett et al., 2004b) and intergeneric levels (e.g., Plunkett et al., 2004c). Because an extensive database of ITS and *trn*L-*trn*F sequences has already been compiled for nearly all genera (and many species) in Araliaceae, these two markers were used in the present assessment of relationships within *Schefflera*. To date, we have been able to sequence both markers from 68 samples of taxa currently referred to this genus, representing 7 of the 10 subgeneric groups recognized by Frodin (Table 1). Using this expanded sampling, our goal is to test the monophyly of *Schefflera* (or to evaluate the extent of its polyphyly) and to identify smaller monophyletic groups that will be suitable for future, more intensive studies, adopting the approach that has recently proven successful for *Polyscias* (Plunkett et al., 2001; see also Eibl et al., 2001; Plunkett et al., 2004b).

Methods and Materials

The combined ITS + *trn*L-*trn*F data set from Plunkett et al. (2004c) included 109 plant samples (representing 108 taxa), 19 of which belong to *Schefflera* s.l. (i.e., *Schefflera* as currently circumscribed). Because this data set comprises a near-comprehensive sampling of the major groups in Araliaceae (encompassing 37 of the 41 currently recognized genera and multiple accessions of all large genera), we used it as a baseline in the present study, to which 49 additional accessions of *Schefflera* s.l. were added. This expanded data set thus includes a total of 68 species of *Schefflera* and 158 terminals overall. Sources of plant tissue for all species of *Schefflera* (plus a single new sample of *Arthrophyllum*) are given in Table 2, along with GenBank accession numbers; information for previously published sequences of other araliad and outgroup taxa is available in Plunkett et al. (2004c, their table 3).

Total DNAs were extracted using the DNeasy Plant Mini kit (QIAGEN Inc.), or using the CTAB method of Doyle and Doyle (1987). Protocols for

amplifying and sequencing newly derived ITS sequences follow Plunkett et al. (2001, 2004b) by amplifying and sequencing the entire ITS region, including the two spacers (ITS1 and ITS2) and the intervening 5.8S rRNA gene. Primers ITS5 (forward) and C26A (reverse) were generally used for both amplification and sequencing, although some taxa required additional or alternative primers, including ITS4 (reverse) or internal primers ITS3 (forward) and the complement of N5.8S (reverse) [= N5.8S-r: 5′–TGC GTT CAA AGA CTC GAT–3′]. For *trn*L-*trn*F, the protocols of Eibl et al. (2001) and Plunkett et al. (2001) were followed, using two external primers ("c" and "f" of Taberlet et al., 1991) for both amplification and sequencing, although one or both internal primers ("d" and "e" of Taberlet et al., 1991) were also required for some taxa. As reported in Eibl et al. (2001), primer "f" has been modified for use in Araliaceae [5′–AAC TGG TGA CAC GAG GAT TTT CAG–3′]. Because most mutations in both ITS and *trn*L-*trn*F were nucleotide substitutions, manual alignment was straightforward.

Separate matrices were assembled from ITS and *trn*L-*trn*F sequence data. In addition, a third matrix was constructed by combining data from both sequences for analysis of congruence and combinability (using the ILD test of Farris et al., 1995). All three matrices were analyzed phylogenetically using PAUP* (version 4, Swofford, 2002) with maximum parsimony (MP). Alignment gaps were treated as missing data, but 19 insertion/deletion events (indels) were scored as binary characters (2 indels were derived from the ITS matrix, and 17 from *trn*L-*trn*F). Early attempts at analyzing each of the three data sets yielded many thousands of shortest-length trees (in excess of 20,000), due apparently to poor resolution of relationships among several large polytomies. Because these analyses quickly exhaust computer memory, we followed the approach described in Plunkett et al. (2001, see also Plunkett et al., 1997) to explore the greatest number of possible tree topologies. In this approach, an initial search of 1000 replicates (with random addition, ACCTRAN optimization, and MULPARS in effect) is executed, saving no more than 100 trees per replicate. The strict consensus from this analysis was then used as a topological constraint for an additional series of searches of 1000 replicates, saving no more than 1000 trees per replicate (and aborting each replicate after saving 1000 suboptimal trees); only trees of the shortest length that do not agree with the original constraint are then saved. An additional approach was used to search for shorter trees in the combined analysis by employing Nixon's (1999) Parsimony Ratchet, implemented using the computer program PAUPRat (Sikes & Lewis, 2001) with a batch of 12 runs (200 replicates/run). To assess confidence in individual clades, bootstrap analyses (Felsenstein, 1985) were executed using 1000 replicates and saving no more than 100 trees per replicate. In addition, the program AutoDecay (Erikson, 1997) was used together with PAUP* to determine decay-index values (Bremer, 1988). MacClade 4 (Maddison & Maddison, 2000) and/or PAUP* were used to assess data fitness and nucleotide compositions for each data set.

Results

Sequence Characteristics

All 158 ITS sequences spanned both spacer regions and the intervening 5.8S rDNA coding region, ranging in total length from 610 to 630 bp. After alignment, the ITS data set included 683 nucleotide (nt) characters and two indel characters, for a total of 685 characters, of which 305 (44.5%) were potentially informative. The *trn*L-*trn*F sequence region included the *trn*L intron and the *trn*L-*trn*F intergenic spacer, ranging in length from 766 to 928 bp. The alignment of these sequences yielded 1082 nt characters, to which 17 indel characters were added, for a total of 1099 characters, 199 (18.1%) of which were potentially informative. We used Kimura's (1980) 2-parameter method to estimate sequence divergence for each data set. Across all taxa, ITS distances ranged from 0 to 34.8%. If outgroup taxa (*Mackinlaya*, *Apiopetalum*, *Myodocarpus*, and *Delarbrea*) are excluded, the maximum divergence drops to 0–28.5%, and if the sequences of *Hydrocotyle* (which have accumulated mutations at a much higher rate) are removed, ITS distances range from 0 to 16.9%. For the *trn*L-*trn*F data set, distances ranged from 0 to 10.4% for all taxa, 0–8.8% for all ingroup taxa, and 0–5.4% among all ingroup taxa except *Hydrocotyle*. The average of all pairwise distances of ITS sequences was 8.5%, indicating that this marker evolves roughly four times faster than *trn*L-*trn*F (2.1%).

Phylogeny Reconstructions

Following the search strategy outlined above, we recovered 20,000 trees with a length of 1852 steps in the MP analysis of the ITS data set. The constraint analysis (using the strict consensus tree) failed to find any shorter trees or any trees not agreeing with the strict consensus, which is presented in Figure 1 with bootstrap (BS) and decay index (DI) values. These trees had a consistency

Table 1. Infrageneric classification of *Schefflera* s.l. proposed by D. G. Frodin (unpublished); all infrageneric names are informal, and are not validly published here. Infrageneric groups under "Sciodaphyllum" are arranged by geographic distribution.

Informal groups of *Schefflera*

Subgeneric groups	Infrageneric groups	Representative species	Distribution
Schefflera	Schefflera	*S. digitata* J. R. Forst. & G. Forst. (type), *S. candelabrum* Baill., *S. pseudocandelabrum* R. Vig., *S. vieillardii* Baill., *S. vitiensis* (A. Gray) Seem.	New Zealand to Vanuatu and Samoa
Plerandra	Canacoschefflera	*S. crassipes* Baill., *S. elongata* Baill.	New Caledonia
	Dictyophlebes	*S. costata* A. C. Sm., *S. dictyophlebia* Frodin	Fiji, Solomon Islands
	Dizygotheca	*S. actinostigma* A. C. Sm. & B. C. Stone, *S. bailloniana* Frodin, *S. elegantissima* (Veitch ex Mast.) Lowry & Frodin, *S. nono* Baill., *S. plerandroides* (R. Vig.) Frodin, *S. reginae* (Linden ex W. Richards) Frodin, *S. toto* Baill., *S. veitchii* (Carrière) Frodin & Lowry	Vanuatu, New Caledonia
	Gabrielleae	*S. gabriellae* Baill., *S. pancheri* Baill., *S. seemanniana* A. C. Sm., *S. vanuatua* Lowry	Vanuatu, Fiji, New Caledonia
	Plerandra	*S. cabalionii* Lowry, *S. insolita* (A. C. Sm.) Frodin, *S. nesopanax* Frodin, *S. pickeringii* (A. Gray) Frodin, *S. stahliana* (Warb.) Frodin	New Guinea to Fiji
Agalma	Agalma	*S. delavayi* (Franch.) Harms, *S. rugosa* (Blume) Harms, *S. wardii* Marquand & Airy Shaw	Asia, Malesia
	Glummea	*S. chapana* Harms, *S. fantsipanensis* Bui, *S. metcalfiana* Merr. ex H. L. Li, *S. pseudospicata* Bui	Asia
	Gynaptenia	*S. aromatica* (Blume) Harms	Malesia
	Heptaphylla	*S. heptaphylla* (L.) Frodin	E/SE Asia, Batan Islands
	Hypoleucae	*S. chinensis* (Dunn) H. L. Li, *S. hypoleucoides* Harms, *S. trevesioides* Harms	Asia
	Unassigned	*S. glabrescens* (C. J. Tseng & G. Hoo) Frodin, *S. heterobotrya* Frodin, *S. macrophylla* (Dunn) R. Vig.	Mainly Asia
Parapanax	Parapanax	*S. avenis* (Miq.) Harms, *S. littoralis* (Miq.) Harms, *S. polita* (Miq.) R. Vig., *S. sarasinorum* Harms ex Koord., *S. simplicifolia* Merr.	Malesia
Cephalopanax	Cephalopanax	*S. cuatrecasasiana* Steyerm., *S. jahnii* (Harms) Steyerm.	Andean South America
Cotylanthes	Cotylanthes	*S. jefensis* M. J. Cannon & Cannon, *S. paniculitomentosa* Cuatrec., *S. quindiuensis* (Kunth) Harms	Panama, NW South America
Crepinella	Crepinella	*S. cracens* Frodin, *S. monosperma* Maguire, Steyerm. & Frodin ex Frodin	N South America
	Unassigned	*S. chimantensis* (Steyerm. & Maguire) Maguire, Steyerm. & Frodin, *S. gleasonii* (Britton & P. Wilson) Alain, *S. spruceana* (Seem.) Maguire, Steyerm. & Frodin, *S. suaveolens* Frodin, *S. umbellata* (N. E. Br.) R. Vig.	N South America

Table 1. Continued.

Informal groups of *Schefflera*			
Subgeneric groups	Infrageneric groups	Representative species	Distribution
Didymopanax	Confusae	*S. confusa* (Marchal) Harms, *S. megacarpa* A. H. Gentry	N South America
	Didymopanax	*S. decaphylla* (Seem.) Harms, *S. morototoni* (Aubl.) Maguire, Steyerm. & Frodin, *S. plurispicata* Maguire, Steyerm. & Frodin, *S. quinquecarinata* Steyerm.	Central & South America
	Unassigned	*S. calva* (Cham.) Frodin & Fiaschi, *S. macrocarpa* (Cham. & Schltdl.) Frodin, *S. malmei* (Harms) Frodin, *S. selloi* (Marchal) Frodin & Fiaschi	E South America
Meiopanax	Meiopanax	*S. bojeri* (Seem.) R. Vig., *S. lukwangulensis* (Tennant) Bernardi, *S. rainaliana* Bernardi, *S. umbellifera* (Sond.) Baill.	Africa, Madagascar
	Vantsilanae	*S. longipedicillata* (Lecomte) Bernardi, *S. macerosa* Bernardi, *S. vantsilana* (Baker) Bernardi	Madagascar
	Unassigned	*S. staufferiana* Bernardi	Madagascar
Sciodaphyllum	Abyssinicae	*S. abyssinica* (Hochst. ex A. Rich.) Harms	Africa
	Barterae	*S. barteri* (Seem.) Harms, *S. goetzenii* Harms	Africa, Seychelles
	Mannii	*S. mannii* (Hook. f.) Harms, *S. volkensii* (Harms) Harms	Africa
	Myriantheae	*S. monophylla* (Baker) Bernardi, *S. myriantha* (Baker) Drake	Africa, Comoros, Madagascar
	Bipalmatifolieae	*S. bipalmatifolia* Merr.	NE Borneo
	Blancoii	*S. blancoi* Merr.	Central Malesia
	Bordenii	*S. bordenii* Merr., *S. bukidnonensis* Merr.	Philippines
	Brassaia	*S. actinophylla* (Endl.) Harms, *S. brassaiella* Ridl., *S. thaumasiantha* Harms, *S. waterhousei* Harms	Mainly New Guinea
	Cephaloschefflera	*S. catanduanensis* Merr., *S. oblongifolia* Merr., *S. ovoidea* Merr.	Philippines
	Elmeri	*S.* "elmeri," nom. unpubl., *S.* "hahliana," nom. unpubl.	Philippines, Sulawesi, New Britain
	Eriocephalai	*S. carrii* Harms, *S. eriocephala* Harms	New Guinea
	Heptapleurum	*S. albido-bracteata* Elmer, *S. arboricola* (Hayata) Merr., *S. brevipes* Merr., *S. caudata* (Vidal) Merr. & Rolfe, *S. elliptica* (Blume) Harms, *S. leucantha* R. Vig., *S. yunnanensis* H. L. Li	Asia, Malesia (to Papuasia and Australia)
	Koordersia	*S. koordersii* Harms	Sulawesi
	Kuchingenses	*S. kuchingensis* Merr., *S. winkleri* Harms	Borneo
	Leytenses	*S. leytensis* Merr.	Philippines
	Multiarcuatae	*S.* "multiarcuata," nom. unpubl.	Borneo
	Multiramoseae	*S. multiramosa* Elmer	Philippines (Mindanao), Sulawesi
	Nodosae	*S. nodosa* (Miq.) F. M. Muell.	Sulawesi
	Obliqueae	*S. obliqua* Merr.	Philippines, Borneo
	Pagiophylla	*S. pagiophylla* Harms, *S. scytinophylla* Harms	New Guinea (western)
	Papuoschefflera 1	*S. bractescens* Ridl., *S. lorentzii* Harms	Mostly New Guinea

Table 1. Continued.

Informal groups of *Schefflera*			
Subgeneric groups	Infrageneric groups	Representative species	Distribution
Sciodaphyllum (continued)	Papuoschefflera 2	*S. forbesii* Ridl., *S. ischnoacra* Harms, *S. porphyranthera* Ridl.	New Guinea
	Papuoschefflera 3	*S. angiensis* Gibbs, *S. bougainvilleana* Harms, *S. chaetorrhachis* Harms	Papuasia
	Papuoschefflera 4	*S. dentata* Frodin, *S. schumanniana* Harms	New Guinea
	Papuoschefflera 5	*S. insculpta* Frodin, *S. straminea* Frodin	New Guinea
	Papuoschefflera 6	*S. polyastra* Harms, *S. setulosa* Harms	New Guinea
	Paratropia 1	*S. beccariana* Harms, *S. hullettii* (King) R. Vig., *S. longifolia* (Blume) R. Vig.	W Malesia
	Paratropia 2	*S. cephalotes* (C. B. Clarke) Harms	W Malesia
	Paratropia 3	*S.* "lanata," nom. unpubl.	NE Borneo
	Paratropia 4	*S. leroyana* C. B. Shang	Vietnam
	Polybotryeae	*S. multifoliolata* Merr., *S. polybotrya* (Miq.) Harms	Malesia
	Protoheptapleurum	*S. insularum* (Seem.) Harms, *S. merrillii* Elmer, *S. petiolosa* (Miq.) Harms, *S. rhynchocarpa* Merr.	Malesia
	Tomentoseae	*S. heterophylla* (Wall. ex G. Don) Harms, *S. schizophylla* (Hance) Frodin, *S. tomentosa* (Blume) Harms	SE Asia, Malesia
	Tribracteolatae	*S. tribracteolata* Bui	Vietnam
	Tupidanthus 1	*S. pueckleri* (K. Koch) Frodin, *S. subintegra* (Craib) C. B. Shang, *S. wallichiana* (Wight & Arn.) Harms	Asia
	Tupidanthus 2	*S. siamensis* W. W. Sm. ex Craib	SE Asia
	Allocotantheae	*S. allocotantha* (Harms) Frodin	Andean South America
	Angulatae	*S. angulata* (Pav.) Harms, *S. euryphylla* Harms, *S. manus-dei* Cuatrec.	Andean South America
	Attenuatae	*S. attenuata* (Sw.) Frodin, *S. glabrata* (Kunth) Frodin, *S. rodriguesiana* Frodin, *S. tremula* (Krug & Urb.) Alain	Middle America, N South America
	Bejucoseae	*S. bogotensis* Cuatrec., *S. tamana* Steyerm.	Venezuela, Colombia
	Cheilodromoi	*S. ayangannensis* Maguire, Steyerm. & Frodin, *S. sessiliflora* Frodin, *S. tremuloidea* Maguire, Steyerm. & Frodin	N South America
	Lasiogynes	*S. lasiogyne* Harms	Colombia, Ecuador
	Minutiflorae	*S. minutiflora* Harms	Andean South America
	Patulae	*S. patula* (Rusby) Harms, *S. stilpnophylla* Harms	Boliva, Peru, Ecuador
	Pentandreae	*S. pentandra* (Pav.) Harms	Peru, Ecuador
	Sciodaphyllum	*S. sciodaphyllum* (Sw.) Harms, *S. sphaerocoma* (Benth.) Harms, *S. systyla* (Donn. Sm.) R. Vig.	Middle and South America
	Unassigned	*S. dielsii* Harms, *S. duidae* Steyerm., *S. sodiroi* Harms	Mainly Andean South America

index (CI, excluding uninformative characters) of 0.340 and a retention index (RI) of 0.711. In the analysis of the *trn*L-*trn*F data set, the same search strategy yielded shortest trees of 572 steps, but the constraint analysis found additional trees (of the same length) that did not agree with the strict consensus. In an iterative approach, we increased the number of saved trees until the constraint analysis failed to find additional MP trees. This process yielded a total of 94,542 trees (CI = 0.630, RI =

0.895). In the strict consensus tree, the Araliaceae clade is well supported (BS = 97%), but relationships within this clade are highly unresolved, forming a large polytomy of 98 small clades (76 clades of a single terminal, 21 clades of 2 to 5 terminals, and a single clade of 13 terminals). Because the major clades of Araliaceae and of *Schefflera* are not resolved, the tree is not shown.

The partition homogeneity (or ILD) test yielded a result of $P = 0.02$, suggesting that the two data sets might not be combinable. It is generally held that data sets should not be combined if there is evidence that they are tracking different phylogenetic hypotheses (i.e., "hard" incongruence) due to mechanisms such as lateral transfer or lineage sorting. However, there are other possible explanations for yielding low ILD results (i.e., "soft" incongruence). Among these are low phylogenetic signal (a form of sampling error) or signal derived from homoplasious substitutions, both of which may be manifested as poor resolution and/or low support among incongruent clades resulting from each partition. Visual inspection of the cladograms based on the separate analyses reveals both a lack of resolution (especially in the *trn*L-*trn*F tree, discussed above) and low support, and we found no examples of incongruence where clade support was above 63% in both trees. This is illustrated by several sets of relationships in the Asian Palmate clade. For example, all of the shortest *trn*L-*trn*F trees suggest a relationship between *Hedera* and *Merrilliopanax*, but this relationship is weakly supported (BS = 61%). In the ITS trees, an apparently incongruent relationship is suggested, in which *Hedera* is sister to the Trevesia + Brassaiopsis clade, and *Merrilliopanax* is sister to *Dendropanax*, but both of these relationships are supported by bootstrap values below 50%. Other possible explanations for incongruence, such as lateral transfer or lineage sorting, are unlikely to play a significant role in the evolutionary history at the level of an entire family. Therefore, we have followed the "total evidence" approach advocated by Kluge (1989; see also Wenzel, 1997; Wenzel & Siddall, 1999) in analyzing the combined data set. In doing so, we note that the resulting tree is better resolved and generally better supported, suggesting that weak phylogenetic signal (as compared to noise) was indeed an issue in each of the separate data sets, and was partially overcome through combination. The combined data set (1784 characters, of which 504 were potentially informative) yielded 20,000 MP trees of 2546 steps (CI = 0.373, RI = 0.736), and the strict consensus of these trees is presented in Figure 2.

The trees presented in Figures 1 and 2 share the same general topology as those resulting from the infrafamilial study of Plunkett et al. (2004c). As already noted, that study was based on a subset of the same data, but with a considerably smaller sample of *Schefflera* species. The combined trees from both studies resolve three major clades within Araliaceae (the Asian Palmate clade, Aralia-Panax clade, and Polyscias-Pseudopanax clade), along with several smaller clades forming a basal polytomy (Cussonia + Seemannaralia, Cheirodendron + Raukaua, two clades of *Schefflera*, and several monogeneric clades such as Osmoxylon and Astrotricha). The separate analysis of ITS data is visually congruent (Fig. 1), but is generally less resolved, with lower clade support (i.e., lower BS and DI values). As indicated above, the *trn*L-*trn*F tree (not shown) provides much less resolution, and none of the three major clades of Araliaceae is reconstructed. However, the *trn*L-*trn*F data are clearly contributing phylogenetic information, as indicated by the slightly increased CI and RI values of the combined tree (compared to those derived from the ITS data alone) and, more significantly, by the increase in support and resolution. This result is especially evident in the basally branching lineages, where support is much higher in the combined trees than in those based on ITS alone. For example, the Araliaceae clade (including *Hydrocotyle*) is supported by a BS of 73% in the ITS tree, but 99% in the combined tree. Both the Polyscias-Pseudopanax and Aralia-Panax clades are left unresolved in the ITS tree, but are resolved and moderately well-supported in the combined tree (BS = 74% and 63%, respectively). There are many additional examples of increased resolution and/or support. This confirms that *trn*L-*trn*F data—although insufficient to provide a resolved consensus tree when analyzed alone—offer a valuable source of additional data when combined with those from ITS sequences.

The combined tree is most germane to the present study. Its topology confirms and expands the findings of earlier analyses regarding the (non-) monophyly of *Schefflera* s.l., which appears to comprise at least five unrelated clades scattered throughout Araliaceae. Two of these (Asian Schefflera and Neotropical Schefflera) are each part of the larger "Asian Palmate clade" (which also includes *Hedera, Brassaiopsis, Trevesia, Heteropanax, Tetrapanax,* and *Fatsia,* among other genera). A third clade, Pacific Schefflera, belongs to the Polyscias-Pseudopanax clade, whereas the remaining two, African-Malagasy Schefflera and Schefflera s. str., are part of the large basal polytomy (although the combined tree fails to unite the type species,

Table 2. Names, sources, and GenBank accession numbers of all ITS and *trn*L-*trn*F sequences of *Schefflera* used in the present study (plus one new sample of *Arthrophyllum*; sources for previously published sequences of other Araliaceae and outgroups are provided in Plunkett at al. 2004c). Voucher and source for ITS and *trn*L-*trn*F from each sample are identical unless otherwise noted. Assignment to informal groups corresponds to the system presented in Table 1.

Species	Voucher/Origin	Informal groups	GenBank accessions	
			ITS	*trn*L-*trn*F
Schefflera s.l.				
Schefflera actinophylla (Endl.) Harms	ITS: *Plunkett 1535* (MO); Queensland, Australia. *trn*L-*trn*F: *Plunkett 1316* (WS), New York Botanical Garden (cult.); native to New Guinea, N Australia	Sciodaphyllum: Brassaia	AF242245	AY393766
Schefflera arboricola (Hayata) Merr.	ITS: *Wen 2478* (F); *trn*L-*trn*F: *Plunkett 1317* (WS), New York Botanical Garden (cult.); native to China (incl. Taiwan)	Sciodaphyllum: Heptapleurum	AF242243	AY955396
Schefflera bailloniana Frodin	*Lowry 4782* (MO); New Caledonia	Plerandra: Dizygotheca	AF396420	AF396415
Schefflera bojeri (Seem.) R. Vig. (1)	*J. Rabenantoandro 357* (MO); Madagascar	Meiopanax: Meiopanax	AY955446	AY955397
Schefflera bojeri (Seem.) R. Vig. (2)	*Lowry 4824* (MO); Madagascar		AY955447	AY955398
Schefflera bractescens Ridl.	*Plunkett 1546* (QRS); Queensland, Australia	Sciodaphyllum: Papuoschefflera 1	AY955448	AY955399
Schefflera candelabrum Baill.	*Lowry 4726* (MO); New Caledonia	Schefflera: Schefflera	AF229728	AY393767
Schefflera costata A. C. Sm.	*Lowry 5512* (MO); Fiji	Plerandra: Dictyophlebes	AY955449	AY955400
Schefflera crassipes Baill.	*Lowry 4797* (MO); New Caledonia	Plerandra: Canacoschefflera	AF229729	AY955401
Schefflera delavayi (Franch.) Harms	*Wen 5021* (F); Sichuan, China	Agalma: Agalma	AY955450	AY955402
Schefflera sp. indet., aff. *dentata* P. Royen	*Lowry 5234* (MO); Indonesia (West Papua)	Sciodaphyllum: Papuoschefflera 4	AY955451	AY955403
Schefflera digitata J. R. Forst. & G. Forst.	*A. Mitchell s.n.* (CHR 485642), Christchurch, New Zealand (cult.); native to New Zealand	Schefflera: Schefflera	U63188	AY393768
Schefflera elegantissima (Veitch ex Mast.) Lowry & Frodin	*Lowry 4715* (MO); New Caledonia	Plerandra: Dizygotheca	AY389050	AF396416
Schefflera elliptica (Blume) Harms (1)	*Plunkett 1525* (CANB); Queensland, Australia	Sciodaphyllum: Heptapleurum	AY955452	AY955404
Schefflera elliptica (Blume) Harms (2)	*Plunkett 1360* (WS), Honlulu Botanical Garden (cult.); native to SE Asia, Queensland		AY955453	AY955405
Schefflera elongata Baill.	*Lowry 4659* (MO); New Caledonia	Plerandra: Canacoschefflara	AY955454	AY955406
Schefflera fantsipanensis Bui	*Lowry 4853* (MO); Vietnam	Agalma: Glummea	AY955455	AY955407
Schefflera gabriellae Baill.	ITS: *Lowry 4648* (MO); New Caledonia. *trn*L-*trn*F: *Lowry 4792* (MO); New Caledonia	Plerandra: Gabrielleae	AF229731	AY393769

Table 2. Continued.

Species	Voucher/Origin	Informal groups	GenBank accessions	
			ITS	*trn*L-*trn*F
Schefflera glabrescens (C. J. Tseng & G. Hoo) Frodin [listed as *Schefflera impressa* (C. B. Clarke) Harms in Plunkett et al., 2004c]	*Wen 5050* (F); Yunnan, China	Agalma: Unassigned	AY389051	AY393770
Schefflera goetzenii Harms	*Lowry 4807* (MO); Zimbabwe	Sciodaphyllum: Barterae	AY955456	AY955408
Schefflera sp. ined., "gordonii" (1)	*Lowry 4674* (MO); New Caledonia	Plerandra: Canacoschefflera	AY955457	AY955409
Schefflera sp. ined., "gordonii" (2)	*Lowry 5541* (MO); New Caledonia		AY955458	AY955410
Schefflera heptaphylla (L.) Frodin	*Lowry 4941* (MO); Vietnam	Agalma: Heptaphylleae	AY955459	AY955411
Schefflera insolita (A. C. Sm.) Frodin [listed as *Plerandra insolita* A. C. Sm. in Plunkett et al., 2004c]	*Lowry 5503* (MO); Fiji	Plerandra: Plerandra	AY389047	AY393756
Schefflera sp. indet., aff. *jahnii* (Harms) Steyerm.	*D. Neill 12609* (MO); Ecuador	Cephalopanax: Cephalopanax	AY955460	AY955412
Schefflera sp. indet., aff. *lasiogyne* Harms	*D. Neill 11935* (MO); Ecuador	Sciodaphyllum: Lasiogynes	AY389055	AY393774
Schefflera sp. indet., aff. *lorentzii* Harms	*Lowry 5248* (MO); Indonesia (West Papua)	Sciodaphyllum: Papuoschefflera 1	AY955461	AY955413
Schefflera lukwangulensis (Tennant) Bernardi	*P. B. Phillipson 5163* (MO); Tanzania	Meiopanax: Meiopanax	AY389052	AY393771
Schefflera macrophylla R. Vig.	*Lowry 4852* (MO); Vietnam	Agalma: Unassigned	AF229733	AY955414
Schefflera sp. ined., "moratiana"	*Lowry 4767* (MO); New Caledonia	Plerandra: Dizygotheca	AY955462	AY955415
Schefflera morototoni (Aubl.) Maguire, Steyerm. & Frodin	*Hammel & Perez 22506* (MO); Costa Rica	Didymopanax: Didymopanax	AY955463	AY955416
Schefflara myriantha (Baker) Drake	*N. A. Mwangulango 501* (MO); Tanzania	Sciodaphyllum: Myriantheae	AY389053	AY393772
Schefflera nesopanax Frodin [listed as *Plerandra vitiensis* (Seem.) Baill. in Plunkett et al., 2004c]	*Lowry 5505* (MO); Fiji	Plerandra: Plerandra	AY389048	AY393757
Schefflera nono Baill.	*Lowry 4731* (MO); New Caledonia	Plerandra: Dizygotheca	AY955464	AY955417
Schefflera pancheri Baill.	ITS: *Lowry 4753* (MO); New Caledonia. *trn*L-*trn*F: *Lowry 4661* (MO); New Caledonia	Plerandra: Gabrielleae	AY955465	AY955418
Schefflera pickeringii (A. Gray) Frodin	*Lowry 5496* (MO); Fiji	Plerandra: Plerandra	AY955466	AY955419

Table 2. Continued.

Species	Voucher/Origin	Informal groups	GenBank accessions	
			ITS	*trn*L-*trn*F
Schefflera plerandroides (R. Vig.) Frodin	*Lowry 4751* (MO); New Caledonia	Plerandra: Dizygotheca	AY955467	AY955420
Schefflera pseudocandelabrum R. Vig.	*Lowry 4795* (MO); New Caledonia	Schefflera: Schefflera	AY389054	AY393773
Schefflera pseudospicata Bui	*Lowry 4916* (MO); Vietnam	Agalma: Glummea	AY955468	AY955421
Schefflera pueckleri (K. Koch) Frodin [listed as *Tupidanthus calyptratus* J. D. Hook. & Thomson in Plunkett et al., 2004c]	*Plunkett 1315* (WS), New York Botanical Garden (cult.); native to SE Asia	Sciodaphyllum: Tupidanthus 1	AF229769	AY393788
Schefflera rainaliana Bernardi	*Lowry 4994* (MO); Madagascar	Meiopanax: Meiopanax	AY955469	AY955422
Schefflera reginae (Linden ex W. Richards) Frodin	*Lowry 4652* (MO); New Caledonia	Plerandra: Dizygotheca	AY955470	AY955423
Schefflera roxburghii Gamble	*Plunkett 1499* (CANB); Queensland, Australia	Sciodaphyllum: Heptapleurum	AY955471	AY955424
Schefflera sp. indet., aff. *sandiana* Harms	*D. Neill 11260* (MO); Ecuador	Sciodaphyllum: Sciodaphyllum	AY955472	AY955425
Schefflera sp. indet., aff. *schultzei* Harms	*Lowry 5252* (MO); Indonesia (West Papua)	Sciodaphyllum: Papuoschefflera 4	AY955473	AY955426
Schefflera seemanniana A. C. Sm. (1)	*Lowry 5511* (MO); Fiji	Plerandra: Gabrielleae	AY955474	AY955427
Schefflera seemanniana A. C. Sm. (2)	*Lowry 5515* (MO); Fiji		AY955475	AY955428
Schefflera sp. indet. (A)	*L. Allorge 1086* (MO); French Guiana	Unassigned	AY955476	AY955429
Schefflera sp. indet. (B)	*L. Allorge 1087* (MO); French Guiana	Unassigned	AY389056	AY393775
Schefflera sp. indet. (C)	*Lowry 5158* (MO); Madagascar	Unassigned	AY955477	AY955430
Schefflera sp. indet. (D)	*Lowry 4840* (MO); Vietnam	Agalma: Unassigned	AY955478	AY955431
Schefflera sp. indet. (E)	*Lowry 4838* (MO); Vietnam	Unassigned (material imperfect)	AY955479	AY955432
Schefflera sp. indet. (F)	*D. Neill 13849* (MO); Ecuador	Sciodaphyllum: Unassigned	AY955480	AY955433
Schefflera staufferiana Bernardi	*G. D. McPherson 17219* (MO); Madagascar	Meiopanax: Unassigned	AY955481	AY955434
Schefflera tomentosa (Blume) Harms	*Lowry 5284* (MO), Bogor Botanical Garden (cult.); native to Thailand, W Malesia	Sciodaphyllum: Tomentoseae	AY955482	AY955435
Schefflera toto Baill. (1)	*Lowry 4727* (MO); New Caledonia	Plerandra: Dizygotheca	AY955483	AY955436
Schefflera toto Baill. (2)	*Lowry 5568* (MO); New Caledonia		AY955484	AY955437
Scheflera trevesioides Harms	*Lowry 4920* (MO); Vietnam [listed as *S. hypoleucoides* in Wen et al. (2001)]	Agalma: Hypoleucae	AF229732	AY393776

Table 2. Continued.

Species	Voucher/Origin	Informal groups	GenBank accessions	
			ITS	*trn*L-*trn*F
Schefflera umbellifera (Sond.) Baill.	*Lowry 4808* (MO); Zimbabwe	Meiopanax: Meiopanax	AF242244	AY393777
Schefflera vantsilana (Baker) Bernardi	*S. Randrianasolo 152* (MO); Madagascar	Meiopanax: Vantsilanae	AY955485	AY955438
Schefflera sp. ined., "veillonorum"	ITS: *Lowry 4784* (MO); New Caledonia. *trn*L-*trn*F: *G. D. McPherson 17801* (MO); New Caledonia	Plerandra: Canacoschefflera	AY955486	AY955439
Schefflera veitchii (Carrière) Frodin & Lowry	*Lowry 4665* (MO); New Caledonia	Plerandra: Dizygotheca	AY955487	AY955440
Schefflera sp. indet., aff. *versteegii* Harms	*Lowry 5254* (MO); Indonesia (West Papua)	Sciodaphyllum: Papuoschefflera 1	AY955488	AY955441
Schefflera vieillardii Baill.	ITS: *Lowry 4747* (MO); New Caledonia. *trn*L-*trn*F: *G. McPherson 17725* (MO); New Caledonia	Schefflera: Schefflera	AY389059	AY393778
Schefflera vitiensis (A. Gray) Seem.	*Lowry 5497* (MO); Fiji	Schefflera: Schefflera	AY955489	AY955442
Schefflera volkensii (Harms) Harms	*P. B. Phillipson 5129* (MO); Tanzania	Sciodaphyllum: Mannii	AY955490	AY955443
Schefflera yunnanensis H. L. Li	*Wen 5028* (F); Yunnan, China	Sciodaphyllum: Heptapleurum	AY389060	AY393779
Schefflera sp. ined., "zollingeriana"	*Lowry 5283* (MO), Bogor Botanical Garden (cult.); native to Java	Sciodaphyllum: Paratropia	AY955491	AY955444
Arthrophyllum				
Arthrophyllum jackianum (G. Don) Frodin	*S. T. Malcomber 3015* (MO); Peninsular Malaysia	N/A	AY955492	AY955445

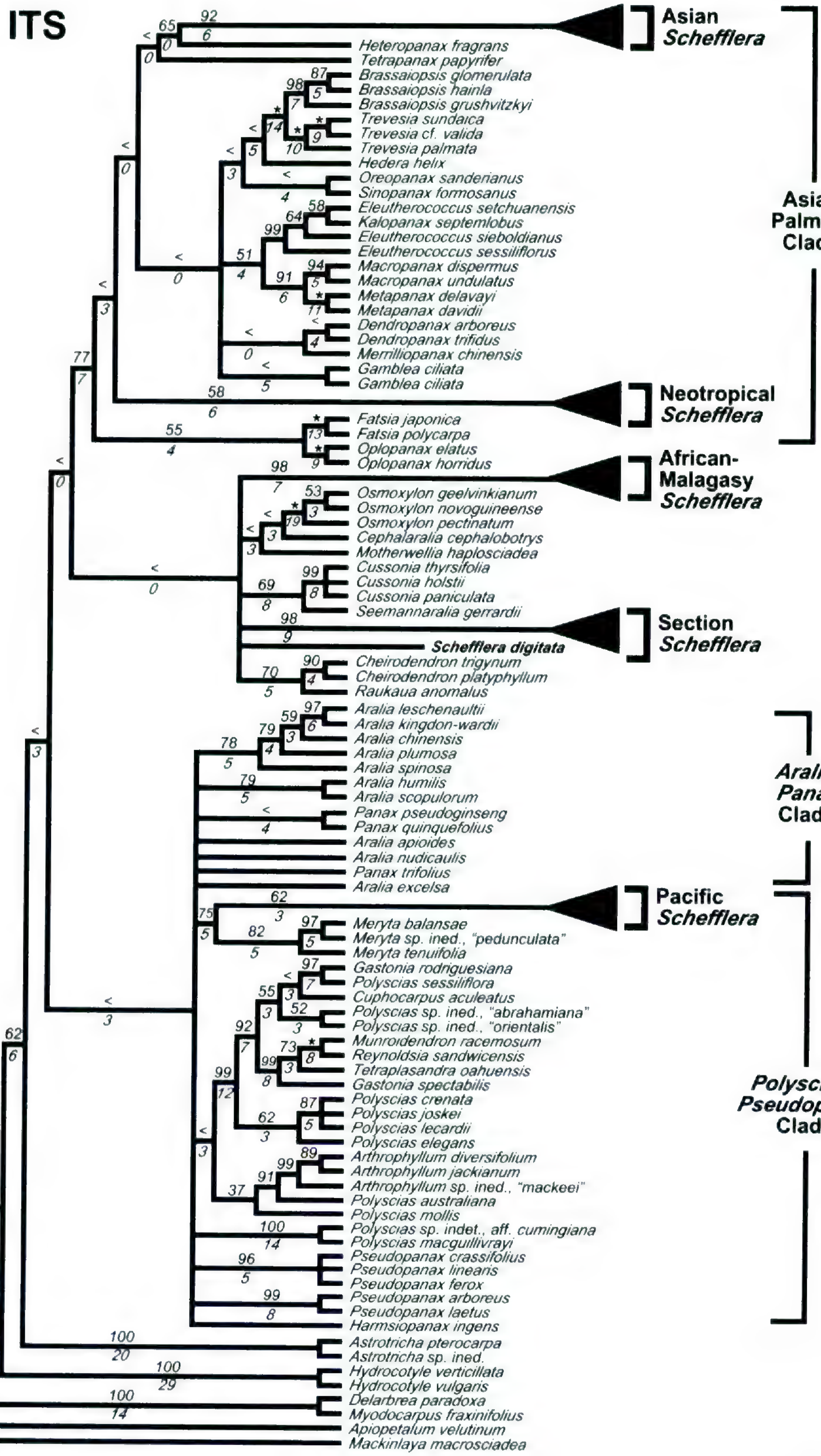

Figure 1. Strict consensus of 20,000 shortest trees (length = 1852 steps) resulting from parsimony analysis of 158 ITS sequences (CI = 0.340; RI = 0.711). Bootstrap percentages are provided above the branches and decay index values are provided below (bootstrap values below 50% are indicated with "<"; those with 100% are indicated with "*"). Major clades discussed in the text are indicated next to brackets. Voucher information for previously published DNA sequences used in this analysis was provided in Plunkett et al. (2004c).

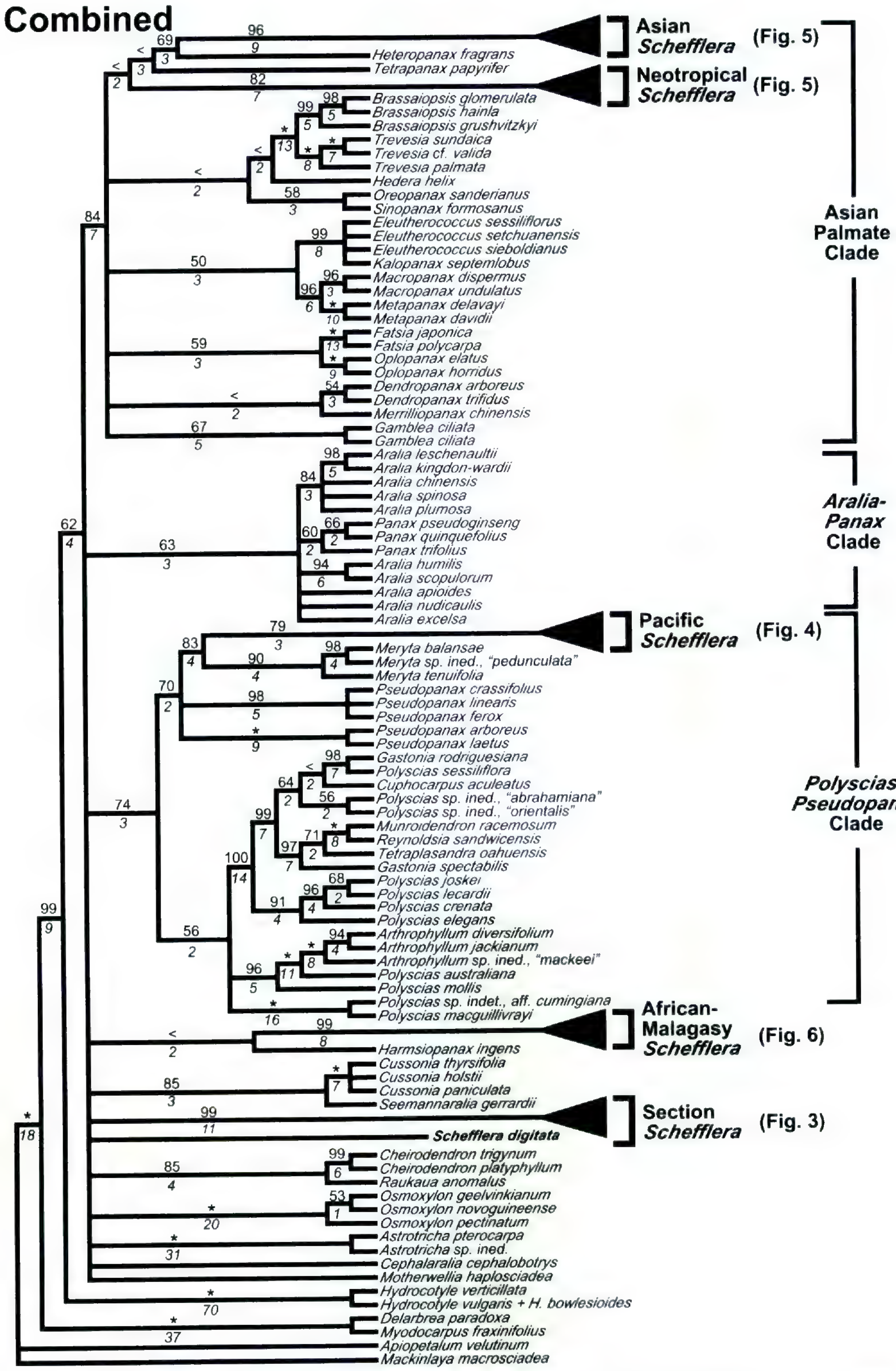

Figure 2. Strict consensus of 20,000 shortest trees (length = 2546 steps) resulting from parsimony analysis of the combined data matrix of 158 ITS and *trn*L-*trn*F sequences (CI = 0.373; RI = 0.736). Bootstrap percentages are provided above the branches and decay index values are provided below (bootstrap values below 50% are indicated with "<"; those with 100% are indicated with "*"). Major clades discussed in the text are indicated next to brackets. Details of relationships within the five major groups of *Schefflera* are provided in Figures 3–6. Voucher information for previously published DNA sequences used in this analysis was provided in Plunkett et al. (2004c).

S. digitata, to the remaining samples of the latter group).

Discussion

Overall relationships among the genera of Araliaceae have been discussed at length by Wen et al. (2001), Plunkett et al. (2004c), and Lowry et al. (2004). Therefore, in the present paper we focus exclusively on relationships within and among the five major clades of *Schefflera*. The phylogenetic trees resulting from the analyses of our molecular data indicate clearly that the genus *Schefflera* is polyphyletic. This finding runs contrary to a basic trend that has developed over the past three decades, in which the circumscription of *Schefflera* has repeatedly been expanded (e.g., Frodin, 1975, 1986, 1989, 1993, 1995; Bernardi, 1969; Maguire et al., 1984; Lowry, 1989; Lowry et al., 1989). The progressive inclusion of numerous, previously recognized segregate genera, plus the description of many new species over the course of the 20th century, have resulted in a dramatic increase in the estimated size of *Schefflera*, from ~150 species (Dalla Torre & Harms, 1900–1907: 363) to ~200 (Willis, 1966, 1973) to roughly 450 (Frodin, 1975: 435) and, at present, 582 named species (Frodin & Govaerts, 2003), with 300 or more species remaining to be named (for a total of about 900; Frodin, 1995). As a result, *Schefflera* (as currently circumscribed) ranks among the most speciose angiosperm genera (cf. *Begonia* (1484 spp.), *Acacia* s.l. (ca. 1325 spp.), *Erica* (860 spp.), and *Ficus* (750 spp.), although *Astragalus* (3270 spp.) far exceeds all others; see Frodin (2004); Maslin et al. (2003)). Our results, however, reveal that the apparent high level of species diversity in *Schefflera* largely represents a taxonomic artifact.

The five clades of *Schefflera* are scattered among all the major lineages of Araliaceae. It would thus appear that the morphological features currently used to recognize a broad *Schefflera* (viz., presence of palmately compound leaves and the absence of articulated pedicels and armaments) either have evolved multiple times or were ancestral in the family. Recent evidence strongly suggests multiple origins of these characters. For example, many studies have identified simple (rather than compound) leaves as ancestral in both Araliaceae and more generally in Apiales (Plunkett et al., 1996, 1997, 2004c; Chandler & Plunkett, 2004; Lowry et al., 2001; Wen et al., 2001). Moreover, recent analyses (Wen et al., 2001; Plunkett et al., 2004c) have concluded that palmately compound leaves evolved multiple times and across all major clades of Araliaceae (e.g., at least once and perhaps two or more times each in the Asian Palmate clade, the Aralia-Panax clade, the Polyscias-Pseudopanax clade, and several smaller clades). Plunkett et al. (2004c) also suggested that articulated pedicels were ancestral in Araliaceae and have been lost repeatedly and in all major clades. The evolution of armaments (such as prickles and barbs) has not been previously examined, but such structures occur in many araliad lineages, including the Asian Palmate clade (e.g., *Eleutherococcus, Kalopanax*, and *Oplopanax*), the Aralia-Panax clade (e.g., some species of *Aralia*), the Polyscias-Pseudopanax clade (e.g., *Polyscias mollis* (Benth.) Harms), and in *Harmsiopanax*, again suggesting multiple origins of this feature. Thus, all three of the characters currently used to define *Schefflera* appear to be highly labile.

Despite the finding of polyphyly in *Schefflera*, our results are by no means a fundamental repudiation of recent studies in this genus. In fact, there is a close correspondence between the five clades we have identified and the major subgeneric groups defined by Frodin (Table 1), suggesting that his interpretations have successfully identified many of the relationships among the species currently placed in *Schefflera*. Moreover, our results do not support the outright reinstatement of the previously recognized segregate genera, most of which would fail the test of monophyly. The studies by Frodin and his coworkers have made crucial advancements in our understanding of inter- and infra-generic relationships, and their work has helped to unite many closely related taxa, including several that had historically been segregated in different genera and even tribes of Araliaceae. For example, in the Asian Schefflera clade alone, the 23 species included in our sample were once placed in at least six genera (viz., *Schefflera, Scheffleropsis, Brassaia, Agalma, Heptapleurum*, and *Tupidanthus*). Likewise, the Pacific Schefflera clade represents species that were once dispersed across four genera (*Schefflera, Plerandra, Dizygotheca*, and *Octotheca*). Despite the rejection of the underlying assumption of monophyly for a broadly defined *Schefflera*, molecular data provide strong evidence for subsuming many of the segregate groups that had been recognized as distinct until the late 20th century.

The molecular data also suggest a perfect correlation between phylogenetic relationships and geographic distributions (a result that we highlight in our choice of informal clade names). Similarly, nearly all of the principal groups recognized in Frodin's system also closely parallel geographic distribution. Two of his informal subgenera ("Schefflera"

and "Plerandra") are restricted to islands in the southwest Pacific, two to Asia and Malesia ("Agalma" and "Parapanax"), four to the Neotropics ("Cephalopanax," "Cotylanthes," "Crepinella," and "Didymopanax"), and one to Africa and Madagascar ("Meiopanax"). The circumscription of each group is in close agreement with our molecular data. For example, Frodin's subgenera "Plerandra" and "Schefflera" correspond perfectly to our Pacific and section Schefflera clades, respectively, and there is a close (but not perfect) correlation between his "Agalma" and "Meiopanax" groups and the Asian and African-Malagasy clades of *Schefflera*. Our current sample is insufficient to evaluate relationships among Frodin's Neotropical subgenera, but it is worth noting that *S. morototoni* ("Didymopanax") and *S. jahnii* ("Cephalopanax") belong to a common broad clade (Neotropical Schefflera).

The single, but notable, exception to the strong correlation between Frodin's subgenera and our results is the geographically widespread "Sciodaphyllum" group. Frodin brought the members of this group together principally on the basis of a "generalized morphology," defined by the presence of unspecialized features exhibited by many Araliaceae, but which are absent (at least in part) in his other subgenera. These features include uniform (non-ruminate) endosperm, limited branching (especially in young individuals of taller species), leaves crowded toward the branch ends, and terminal paniculate inflorescences that often have elongated secondary axes bearing numerous high-order inflorescence units (umbellules, heads, racemules, spicules, etc.). In our analysis, representatives of this subgeneric group from Africa/Madagascar (*S. goetzenii, S. myriantha, S. volkensii*), the New World (*S. lasiogyne, S. sandiana*), and Asia (*S. actinophylla, S. arboricola, S.* sp. indet., aff. *dentata, S. elliptica, S. heptaphylla, S. lorentzii, S.* sp. indet., aff. *schultzei, S. pueckleri, S. versteegii, S. roxburghii, S.* sp. ined., "zollingeriana") do not form a single clade, but instead are found within the three geographically defined clades among the samples from other subgenera. Thus, for example, African-Malagasy members of "Sciodaphyllum" are sister to the African-Malagasy "Meiopanax" group rather than to representatives of "Sciodaphyllum" from other geographic regions (see Figs. 5, 6).

Notwithstanding the polyphyly of the "Sciodaphyllum" group, the overall pattern of agreement between Frodin's system and our results is supported by many additional lines of evidence. In the following sections, we explore the composition of each major clade and the morphological and geographic characters that appear to support them.

THE NOMINATE SECTION

The generitype of *Schefflera, S. digitata,* shares a distinctive morphology with seven other species from the insular Pacific (Lowry, 1989). These form a group that has been regarded variously as *Schefflera* s. str. (Seemann, 1865: 175–176; Lowry, 1989), *Schefflera* sect. *Schefflera* (first referred to by the superfluous sectional name *Euschefflera* by Harms (1894–1897)), or subgenus "Schefflera" in Frodin's informal system (Table 1). In addition to *S. digitata* (from New Zealand), the group includes three species endemic to New Caledonia (*S. vieillardii, S. candelabrum,* and *S. pseudocandelabrum*), two from Fiji (*S. vitiensis* and *S. euthytricha* A. C. Sm.), and one species each from Vanuatu and Samoa (*S. neoebudica* Guillaumin and *S. samoensis* (A. Gray) Harms, respectively) (Lowry, 1989; see also Smith & Stone, 1968; Smith, 1985). All are shrubs or small understory trees, commonly branching near the base and having a bushy appearance when fully grown. The species are further characterized by paniculate inflorescences bearing numerous umbellules, racemules, or spicules of small, bisexual, 5- to 10-carpellate flowers with free styles that persist in fruit. Moreover, in a survey of the wood anatomy of New Caledonian *Schefflera,* Oskolski and Lowry (2001) found that members of this group have highly distinctive features, including very large rays and abundant septate fibers.

In our molecular analysis we have sampled five of the eight species in the group. In the MP trees (see Figs. 1–3), *S. digitata* is left unresolved and perhaps excluded from the clade that unites the remaining four samples (BS = 99%, DI = 11 in the combined tree; Fig. 3), but both neighbor-joining and parsimony bootstrap trees (not shown) suggest a relationship among all five of these species, and their distinctive morphology leaves little doubt regarding the monophyly of this group. From a nomenclatural standpoint, it is an unfortunate accident of history that the smallest of the five clades of *Schefflera* includes the type species, necessitating transfers, reinstatements, or new combinations for nearly 600 already named and accepted species.

PACIFIC *SCHEFFLERA*

A second clade of *Schefflera* contains species that are also restricted to islands in the southwest Pacific (BS = 79%, DI = 3 in the combined tree; Figs. 2, 4), but are morphologically distinct from

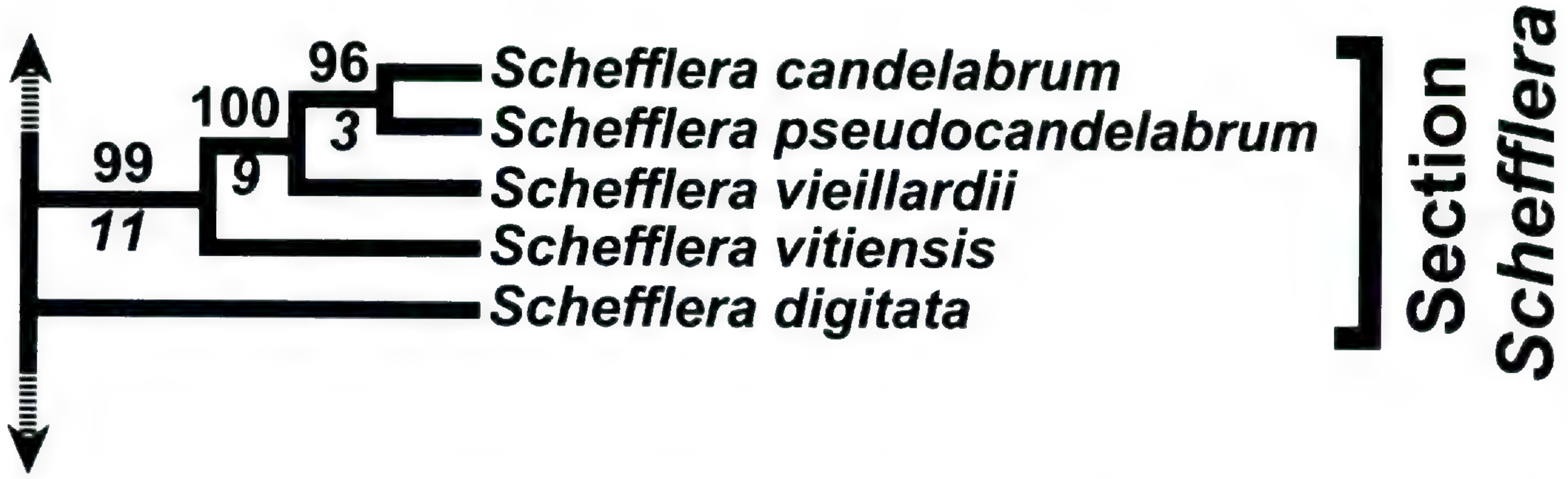

Figure 3. Details of relationships of the Schefflera sect. Schefflera group from the combined analysis of ITS and *trn*L-*trn*F sequences. The basal node indicates the polytomy at the base of the broader Araliaceae clade (Fig. 2). Bootstrap percentages are provided above the branches and decay index values are provided below.

members of the type section. In our sample, this "Pacific Schefflera" clade is represented by species from New Caledonia and Fiji, but additional closely related species are found in New Guinea, the Solomon Islands, and Vanuatu (Lowry, 1989; see also Smith & Stone, 1968; Smith, 1985; Philipson, 1995). There is perfect agreement between this clade and Frodin's circumscription of subgenus "Plerandra." On the whole, the Pacific Schefflera clade is united by the presence of compound-umbellate or paniculate-umbellate inflorescences with relatively large flowers (compared to the type section) borne in umbellules, and usually an andromonoecious sexual system. The New Caledonian members of this clade also share a similar suite of wood anatomical features (Oskolski & Lowry, 2001).

Various authors have recognized a number of well-defined subgroups among the members of this clade, two of which have been retained by many recent workers. The segregate genus *Plerandra*, which ranges from New Guinea to Fiji, was established in 1854 to accommodate species whose stamens are more numerous than the petals (as well as delayed inflorescence development). However, this form of anisomery has evolved multiple times in Araliaceae (Plunkett et al., 2004c) and is a defining feature of several other genera (including *Tupidanthus*, another segregate of *Schefflera*; see Tseng, 1973). Three Fijian members from this group were included in our sample: *Schefflera pickeringii* (the type species of *Plerandra*), *S. insolita*, and *S. nesopanax* (= *Plerandra vitiensis*). Similarly, *Dizygotheca* was recognized at the generic level in 1892 (but earlier and independently in 1878 as *Plerandra* sect. *Pentadiplandra*) to accommodate a distinctive group of mainly New Caledonian species that have anthers with eight thecae (vs. the usual four observed in all other Araliaceae), and now also known to be tetraploid (cf. Lowry, 1986; Yi et al., 2004). Members of this group have distinctive inflorescences with a paniculate-umbellate structure (Lowry, 1989; Oskolski & Lowry, 2001), and usually have flowers with relatively long, free styles. Our sample includes seven species from the Dizygotheca group (viz., *S. bailloniana*, *S. elegantissima*, *S.* sp. ined., "moratiana," *S. nono*, *S. plerandroides*, *S. reginae*, *S. toto*, and *S. veitchii*), all from New Caledonia, although the group also has members in Vanuatu (Lowry, 1989). *Schefflera plerandroides* has also been placed in the segregate genus *Octotheca* by some authors (e.g., Viguier, 1906, 1925; Guillaumin, 1948; Hutchinson, 1967) because of its polymerous androecium and gynoecium, with 10, 15, or 20 stamens and carpels (vs. 5 stamens and 5 to 10 carpels in other members of *Dizygotheca*). However, *S. plerandroides* otherwise shares all of the features that characterize *Dizygotheca* (see Oskolski & Lowry, 2001), and as indicated above, the evolution of polymery in Araliaceae has been shown to have occurred independently multiple times (Plunkett et al., 2004c).

Three additional, morphologically distinct groups (all unpublished) also form part of the Pacific Schefflera clade. The first group, "Gabrielleae" (three species sampled, *S. gabriellae* and *S. pancheri* from New Caledonia, and *S. seemanniana* from Fiji), is characterized by calophyllous venation (i.e., leaflets with numerous parallel secondary veins), compound umbellate inflorescences featuring duodichogamy, short styles fused to form a small beak, and fruits with 5 to 10 pyrenes. The second group, "Dictyophlebes" (one species sampled, *S. costata* from Fiji), is similar to "Gabrielleae," but the inflorescences do not exhibit duodichogamy, the fruits remain inferior through maturity, the stylar column is shorter and thicker, and in the fruit-body the

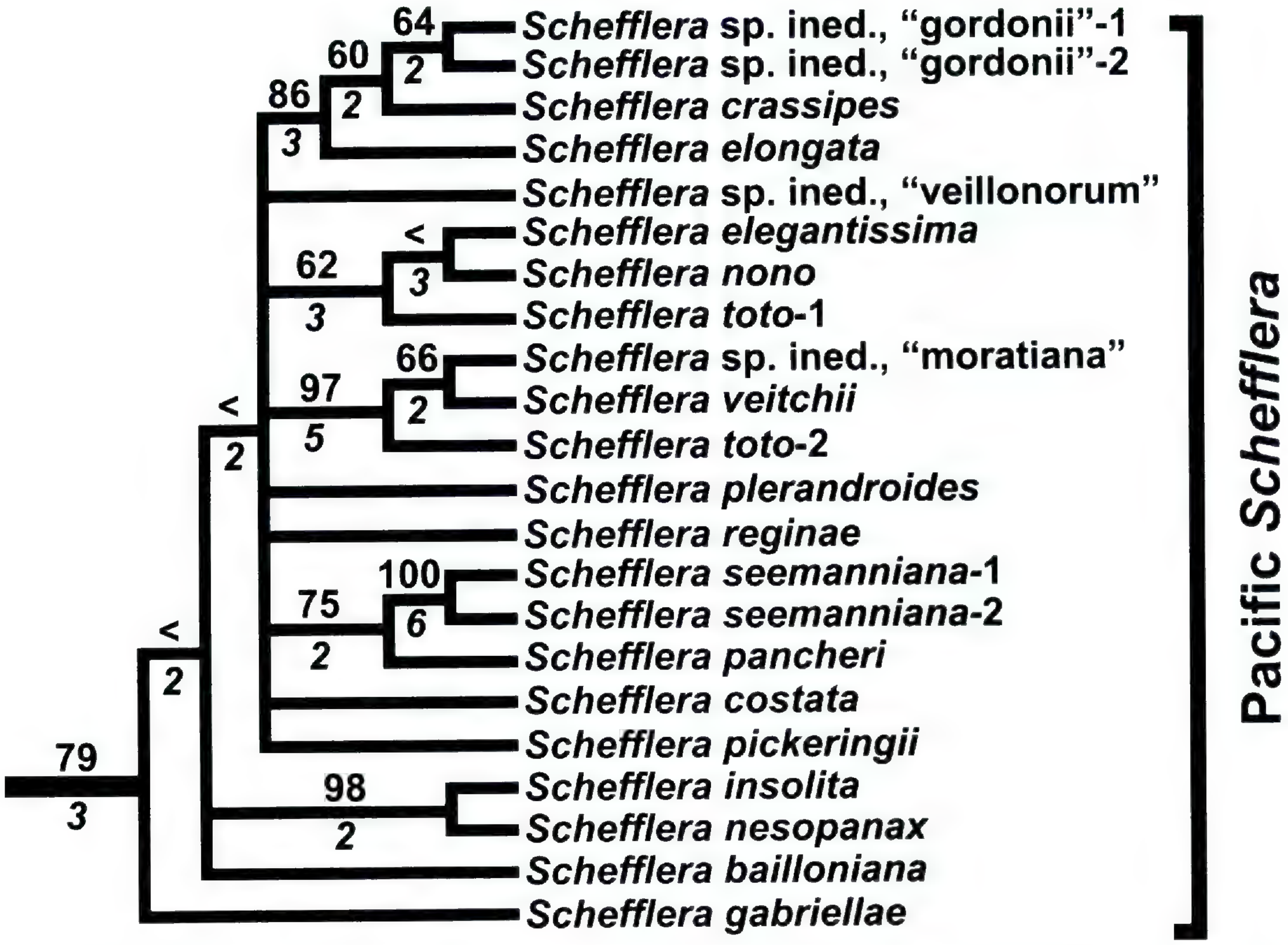

Figure 4. Details of relationships within the Pacific Schefflera clade from the combined analysis of ITS and *trn*L-*trn*F sequences (see Fig. 2). Bootstrap percentages are provided above the branches and decay index values are provided below (bootstrap values below 50% are indicated with "<").

number of locules (and pyrenes) ranges up to 12. The last group in the Pacific Schefflera clade, with four species sampled here (*S. crassipes*, *S. elongata*, *S.* sp. ined., "gordonii," *S.* sp. ined., "veillonorum"), comprises the New Caledonian endemic section "Canacoschefflera." This group is characterized by coriaceous leaves, once- or twice-umbellate inflorescences, flowers with relatively long styles that are either free or basally united, and fruits with 3 to 5 pyrenes (Oskolski & Lowry, 2001). Overall, relationships among the five groups comprising the Pacific Schefflera clade remain somewhat obscured by low support and poor resolution at the base of this clade. Nonetheless, several subclades encompassing smaller groupings of species are relatively well resolved and closely correspond to the informal sections and segregate genera.

ASIAN *SCHEFFLERA*

The Asian Schefflera clade (BS = 96%, DI = 9 in the combined tree; Figs. 2, 5) unites all 23 taxa sampled from Asia and Malesia, including those extending into northern Queensland, Australia (such as *S. actinophylla* and *S. elliptica*). This clade includes all of the species we sampled belonging to Frodin's subgenus "Agalma," as well as all of the Asian taxa sampled from his large, geographically heterogeneous subgenus "Sciodaphyllum." Within the Asian Schefflera clade, these two groups correspond to two subclades (although they are weakly supported; BS ≤ 50%; Fig. 5), with only three exceptions (*Schefflera* sp. indet. D-*Lowry 4840*, *S. heptaphylla*, and *S. trevesioides*), which are placed among the members of "Sciodaphyllum" even though they have a morphology that suggests they belong in the "Agalma" group. The Asian Schefflera clade also includes species once referred to several other segregate genera, including *Brassaia* (distinguished by having large paniculate inflorescences with sessile flowers borne in dense heads, ovaries with 10 to 12 carpels, and sessile stigmas) represented in our study by *S. actinophylla*, and *Tupidanthus* (characterized by very high stamen and carpel number, sometimes exceeding 100), represented by *S. pueckleri*.

Frodin (unpublished data) hypothesized a close

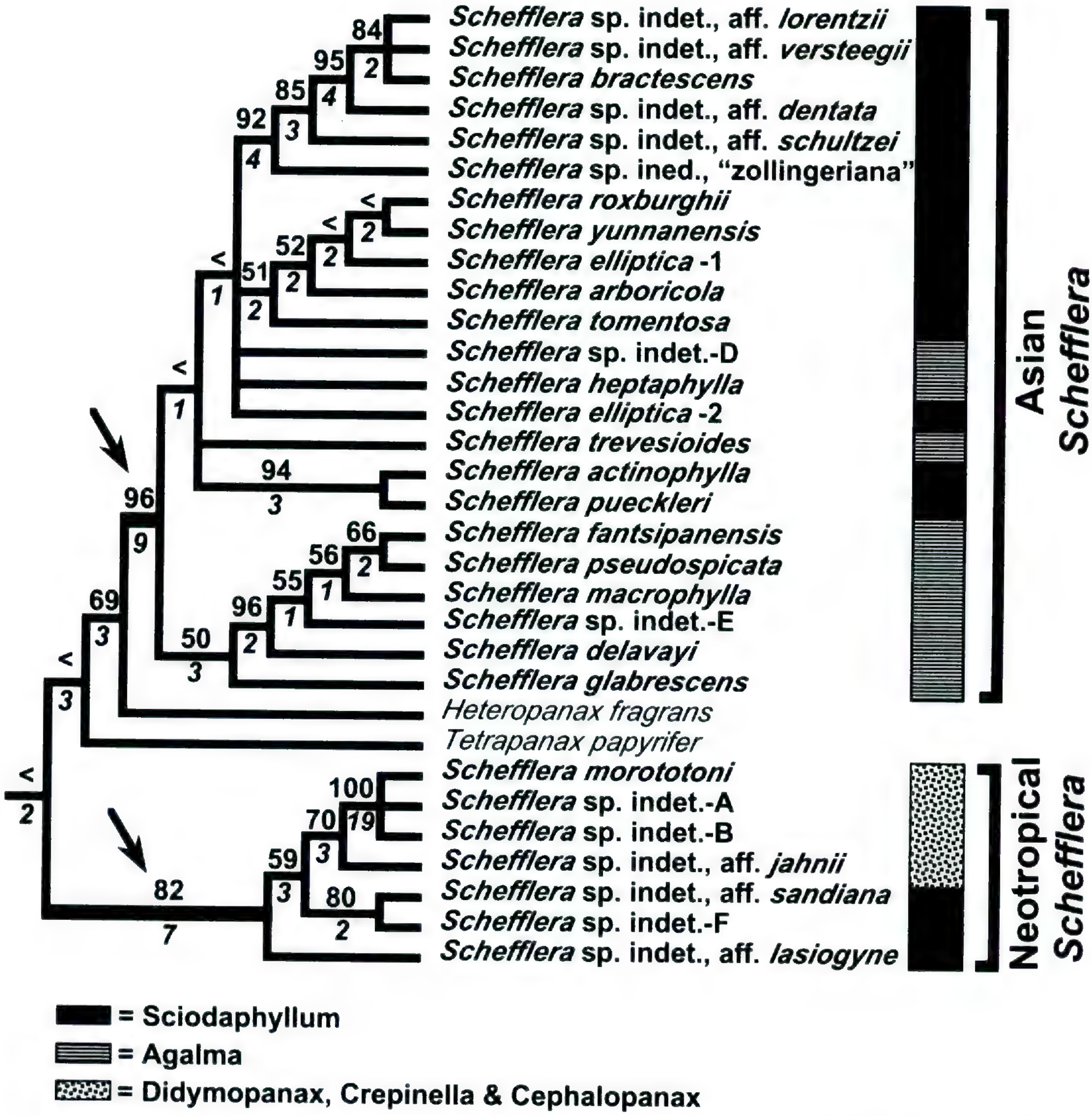

Figure 5. Details of relationships within the Asian and Neotropical Schefflera clades from the combined analysis of ITS and *trn*L-*trn*F sequences (see Fig. 2). Bootstrap percentages are provided above the branches and decay index values are provided below (bootstrap values below 50% are indicated with "<"). Correspondence between the molecular-based phylogeny and the informal, morphologically based classification system (Table 1) are indicated with solid, cross-hatched, and stippled boxes.

affinity between the Brassaia and Tupidanthus groups, an idea that is supported by our results (BS = 94%, DI = 3; Fig. 5). Similarly, our data support a close relationship (BS = 92%, DI = 4; Fig. 5) between Frodin's "Papuoschefflera" group (represented by five samples from New Guinea) and the mainly Sundan "Paratropia" group (represented by *S.* sp. ined., "zollingeriana"), again confirming earlier ideas proposed by the third author. Taken together, these findings further reinforce Frodin's notion that "Sciodaphyllum" represents a morphological grade. It must be emphasized, however, that much broader sampling is needed before a clear picture of alliances within Asia and Malesia can be drawn.

NEOTROPICAL *SCHEFFLERA*

The generic-level diversity of Araliaceae in the Neotropics is quite low, with only four genera currently recognized (see Lowry et al., 2004; Plunkett et al., 2004c; Frodin & Govaerts, 2003), but this masks a very high level of species diversity, including many taxa currently assigned to *Schefflera*

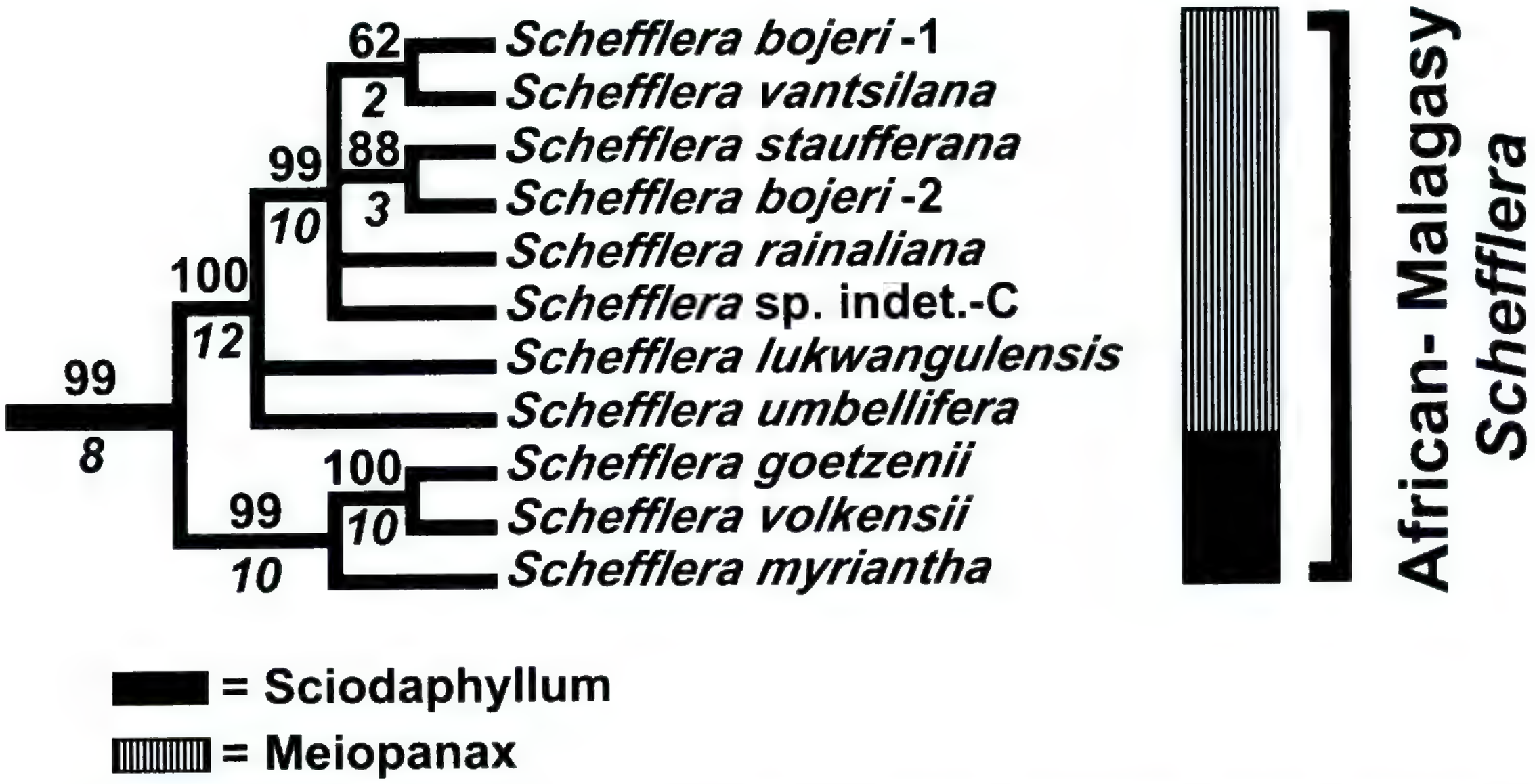

Figure 6. Details of relationships within the African-Malagasy Schefflera clade from the combined analysis of ITS and *trn*L-*trn*F sequences (see Fig. 2). Bootstrap percentages are provided above the branches and decay index values are provided below. Correspondence between the molecular-based phylogeny and the informal, morphologically based classification system (Table 1) are indicated with solid and cross-hatched boxes.

(Maguire et al., 1984; Frodin, 1995). Although our sampling is rather limited (seven species), it nevertheless suggests that the Neotropical species of *Schefflera* form a single clade (BS = 82%, DI = 7 in the combined tree; Figs. 2, 5). As in previous studies of Araliaceae based on a smaller data set (e.g., Plunkett et al., 2004c), the Neotropical Schefflera clade is part of the broader Asian Palmate clade. This type of trans-Pacific distribution occurs in two other parts of the Asian Palmate clade, between the eastern Asian genus *Sinopanax* and the Neotropical *Oreopanax,* and also within *Dendropanax,* which has representatives on both continents. This pattern of disjunction may provide evidence of a boreotropical history for the Asian Palmate clade of Araliaceae (see Wolfe, 1975; Tiffney, 1985; Lavin & Lucklow, 1993; Wen, 1999, 2001a; Fritsch, 2001), although long-distance dispersal across the Pacific cannot be ruled out.

As indicated above, the Neotropical clade includes five subgeneric groups in Frodin's system (Table 1), "Cephalopanax," "Cotylanthes," "Crepinella," "Didymopanax," and "Sciodaphyllum." All are woody, but "Cotylanthes" comprises exclusively non-free-standing taxa, while members of "Cephalopanax," "Crepinella," and "Didymopanax" are entirely terrestrial and free-standing. Neotropical "Sciodaphyllum" encompasses a range of habits, with many members at least sometimes hemi-epiphytic. "Cephalopanax," including *S.* sp. indet., aff. *jahnii,* all occur at relatively high elevations and feature palmately compound leaves with thick leaflets and paniculate, generally twice-compound inflorescences with a distinct main axis, small bracts, flowers arranged in heads, and a 2-locular ovary. Members of the "Didymopanax" group, including *Schefflera morototoni,* are generally found at low to mid-elevations and have mostly palmately compound leaves (although in *S. lucumoides* (Decne. & Planch. ex Marchal) Frodin & Fiaschi they are somatically unifoliolate) with leaflets of varying form and thickness, and small bracts; many species also have a distinctively sericeous indumentum. The inflorescences are more or less paniculate, once- to thrice-compound, and mostly lack a distinct main axis (and often becoming pseudolateral), the flowers are borne in umbellules or racemules, and the 2(to 5)-locular ovaries have largely free styles that recurve at maturity. The "Crepinella" group (not included in our sample) comprises species primarily from higher elevations (except for *S. japurensis* (Mart. & Zucc. ex Marchal) Harms and *S. spruceana* (Seem.) Maguire, Steyerm. & Frodin). The leaves are palmately compound or unifoliolate (as in *S. hitchcockii* (Lasser & Maguire) Maguire, Steyerm. & Frodin) and generally have thick leaflets with closely spaced lateral veins. The inflorescences are compound-umbellate (similar to "Plerandra"), sometimes to four or more degrees, have small bracts, and frequently exhibit duodichogamy. The ovaries are 2- to 5-locular and the styles are mostly united into a column. Species in the "Co-

tylanthes" group occur at mid-elevations and are completely glabrous. Their leaves are palmately compound and their bracts are large. Members of "Cotylanthes" have paniculate, few-branched inflorescences with flowers that are borne in racemosely arranged umbellules, with 5- to 10-locular ovaries, and entirely free styles. Finally, species of "Sciodaphyllum" from the Neotropics—as in other parts of the world—have generally compound leaves (spectacularly so in some species, such as *Schefflera diplodactyla*, with its very large and poly-compound leaves, and *S. sciodaphyllum* (Sw.) Harris, which has bundle-compound leaves) that are glabrous to variously pubescent (but with indument that differs from those found in Old World taxa). Members of this group generally have inflorescences that are terminal and paniculate with few to many primary branches and quite conspicuous bracts, flowers that are borne in fascicles, umbellules, capitula, racemules or spicules (which in turn are either sessile or pedunculate and racemosely arranged along the more or less elongate branches), and ovaries that are usually 3- to 8(most commonly 5)-locular.

AFRICAN-MALAGASY *SCHEFFLERA*

All of the 11 species of *Schefflera* sampled from Africa and Madagascar form a single clade in the combined tree (BS = 99%, DI = 8; Figs. 2, 6). Within this African-Malagasy Schefflera clade, there are two well-supported subclades, each of which has members both in continental Africa and in Madagascar. One corresponds exactly to Frodin's subgenus "Meiopanax" (BS = 100%, DI = 12; Fig. 6), characterized by an entirely terrestrial habit, usually rather coriaceous leaflets (which tend to dry dark), small fused stipules that are either eligulate or have only a small ligule, paniculate to compound-umbellate inflorescences often with persistent, indurated, partially empty bracts, rather small flowers in racemose, spicate, or umbellate arrangements, very small, free styles, 2- to 5-locular ovaries, transversely round or somewhat compressed (but never flattened) fruit, and smooth or pseudoruminate endosperm. The second subclade corresponds to the African-Malagasy elements of Frodin's morphologically generalized "Sciodaphyllum," whose morphology is similar to that described above for Neotropical species, although *S. myriantha* has multi-compound inflorescences with a compound-umbellate tendency.

THE FUTURE OF *SCHEFFLERA*

The present study is based on a significantly expanded sample of *Schefflera* compared to other recent phylogenetic analyses of Araliaceae (e.g., Wen et al., 2001; Plunkett et al., 2004c). However, with an estimated 900 described and undescribed species, the 68 taxa of *Schefflera* examined here represent less than 8% of the genus. This limitation, coupled with the extent of polyphyly (and parallelism) in *Schefflera*, precludes any formal taxonomic recircumscriptions; these must await more comprehensive analyses. The results presented here are thus best viewed as working hypotheses that can serve as a starting point for more intensive testing. To that end, we have initiated studies to expand overall sampling within each of the five major clades of *Schefflera*. Because these clades are spread throughout Araliaceae, each analysis will have to be completed within the broader context of the entire family. This approach will permit us to verify the monophyly of each clade, to examine relationships within each of them, to explore the possibility that additional, unrelated clades may also be discovered as our sampling is expanded, and to re-evaluate our conclusion that these clades are strongly correlated with geographic distribution. The task is most challenging for the Asian and Neotropical clades, which (if confirmed to be monophyletic) represent 200 to 300 and 500+ species, respectively. At the other extreme, the type section encompasses only eight species (Lowry, 1989), and the remaining two clades (Pacific Schefflera and African-Malagasy Schefflera) each comprise 40 to 50 species. We have already successfully implemented a similar strategy for evaluating the second largest genus of Araliaceae, *Polyscias*, which was initiated by a broad study of the genus (Plunkett et al., 2001) and is now being followed by more focused analyses of individual subclades (Eibl et al., 2001; Plunkett et al., 2004b; see also Costello & Motley, 2001). The last of these will soon be completed, permitting a comprehensive re-evaluation of that genus. Although the task in *Schefflera* will be considerably more difficult, it seems ideally suited to the stratified approach developed for *Polyscias*. Given the scattering of *Schefflera* clades across Araliaceae, the results of future research will play a critical role in our effort to establish a new infrafamilial classification system for the family based on monophyletic genera that can be easily recognized using morphological and biogeographic features.

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A REVISION OF *DIDYMODON* SECTION *FALLACES* (MUSCI, POTTIACEAE) IN EUROPE, NORTH AFRICA, MACARONESIA, AND SOUTHWEST AND CENTRAL ASIA[1]

Juan A. Jiménez, Rosa M. Ros, María J. Cano, and Juan Guerra[2]

Abstract

Didymodon sect. *Fallaces* (Musci, Bryopsida) is taxonomically revised for Europe, North Africa, Macaronesia, and Southwest and Central Asia. Nine species are recognized. *Didymodon planotophaceus, D. spadiceus* var. *siluricus,* and *Didymodon ceratodonteus* are newly synonymized with *D. tophaceus*; *D. barbuloides* is a new synonym referred to *D. spadiceus,* and *Trichostomum rigidulum* var. *paludosa* to *D. fallax.* Lectotypes for *Barbula adriatica, B. falcifolia, B. insidiosa, B. kneuckeri, B. rigidicaulis, B. serpenticaulis, B. sinensi-fallax, Didymodon barbuloides, D. bosniacus, D. giganteus, D. levieri, D. maximus, D. rufus, D. spadiceus, D. spadiceus* var. *siluricus, D. tophaceus, D. tophaceus* var. *breidleri, Limneria viridula,* and *Trichostomum rigidulum* var. *paludosa* are designated here. *Didymodon asperifolius* and *D. tophaceus* are reported for the first time from the Caucasus and Mauritania respectively. Descriptions, a taxonomic key, as well as LM and SEM photographs are included.

Key words: Asia, *Didymodon,* Europe, Macaronesia, North Africa, Pottiaceae, taxonomy.

Didymodon Hedw. is a genus of the moss family Pottiaceae that includes approximately 122 species worldwide, with the greatest diversity in temperate and mountainous regions (Zander, 1993). The genus was described by Hedwig (1801) to include three species, only one of which is currently accepted in the genus: *D. rigidulus.* The remaining species correspond to genus *Ditrichum* Hampe.

The genus concept of *Didymodon* has been in dispute, especially as regards the morphological delimitation of *Didymodon* versus *Barbula* Hedw. The taxonomic differences between the two genera have long been based on peristome characters: in *Barbula* formed by long and twisted teeth and in *Didymodon* by short and straight teeth. Since these characters separated gametophytically closely related species of the genus *Didymodon* and *Barbula* (e.g., *D. fallax* and *D. spadiceus*), the differentiation between both genera was generally abandoned (Dixon, 1924; Mönkemeyer, 1927; Hilpert, 1933; Chen, 1941; Nyholm, 1989; Smith, 1978; Kürschner, 2000). Saito (1975) differentiated *Didymodon* and *Barbula* for the first time by gametophytic characters. He principally used the axillary hairs of the leaves for discriminating both genera. The axillary hairs in *Didymodon* have one or two brown basal cells, while in *Barbula* the hairs are hyaline throughout. Later Zander (1993), in his world monograph of the Pottiaceae, expanded the delimitation between *Didymodon* and *Barbula.*

Besides this controversy concerning *Barbula,* the segregation of some *Didymodon* species into other closely related genera, such as *Geheebia* Schimp., *Oxystegus* (Limpr.) Hilp., *Husnotiella* Cardot, and *Trichostomopsis* Cardot, is also of note. However, according to Saito (1975) and Zander (1978, 1993) all of these have the morphological features assigned to *Didymodon.* The molecular data support this opinion. Werner et al. (2004a) sequenced cp *rps*4 of *Didymodon rigidulus* Hedw., *Geheebia gigantea* (Funck) Boulay, *Oxystegus sinuosus* (Mitt.)

[1] We thank the curators of the herbaria and the collectors who sent us material on loan: B, BCB, BM, BP, BR, C, CAIA, CAME, CANM, CGE, CLU, COI, DUKE, E, FCO, FI, G, GB, GDA, GJO, GZU, H, HBG, IRAN, JE, L, LE, LISU, M, MA, MO, MUB, NMW, NY, O, PAMP, PC, PO, PRC, RO, S, SINU, SOM, VAL, VIT, W, WB, WU, Z, herbarium T. L. Blockeel, herbarium A. Cogoni, herbarium R. Düll, herbarium W. Frey, herbarium J. Martínez-Abaigar, herbarium R. B. Pierrot, herbarium M. Sabovljevic, herbarium R. Skrzypczak, herbarium C. C. Townsend. This work has been carried out with financial support from MCYT of Spain (Projects BOS2001-0276 and BOS2000-0296-C03-01) and "Fundación Séneca" of Murcia (PI-15/00762/FS/01).

[2] Departamento de Biología Vegetal, Área de Botánica, Facultad de Biología, Campus de Espinardo, E-30100 Murcia, Spain. jajimene@um.es.

Hilp., and *Trichostomopsis australasiae* (Hook. & Grev.) H. Rob and observed that all these species are closely related. More precise data have been obtained when sequencing the nrITS region of a high number of taxa, which show that the genus *Didymodon* is monophyletic after including the formerly segregated species and is clearly separated from *Barbula* (Werner et al., 2004b, 2005).

According to Zander (1993) *Didymodon* consists of five sections: section *Asteriscium* (Müll. Hal.) R. H. Zander, section *Fallaces* (De Not.) R. H. Zander, section *Rufidulus* (Chen) R. H. Zander, section *Didymodon*, and section *Vineales* (Steere) R. H. Zander.

Studies of *Didymodon* in Europe are scant, even if we include those of Düll (1984), Düll-Hermanns and Düll (1985), and Kučera (2000), on central European species, and of Kučera (2002), on northern European species. No study has until now included North African taxa or those from Central and Southwest Asia. Recent years have seen the publication of floristic studies or checklist studies in this area (Frey & Kürschner, 1991; Ros et al., 1999; El-Saadawi et al., 1999; Kürschner, 2000; Cano et al., 2002), which have pointed to the existence of numerous endemisms and taxa described or collected once during the first half of the 20th century and then forgotten. Many more works have been published on this genus in North America and Mexico (Zander, 1978, 1981, 1994), East Asia (Chen, 1941), and Japan (Saito, 1975; Noguchi, 1988).

Recognizing the overall scarcity of information, we have carried out a taxonomic revision of the section *Fallaces* in Europe, North Africa, Macaronesia, and Southwestern and Central Asia. Nine species belong to this section in this geographic area: *Didymodon asperifolius* (Mitt.) H. A. Crum, Steere & L. E. Anderson, *D. fallax* (Hedw.) R. H. Zander, *D. ferrugineus* (Schimp. ex Besch.) M. O. Hill, *D. giganteus* (Funck) Jur., *D. maschalogena* (Renauld & Cardot) Broth., *D. maximus* (Syed & Crundw.) M. O. Hill, *D. spadiceus* (Mitt.) Limpr., *D. tomaculosus* (Blockeel) M. F. V. Corley, and *D. tophaceus* (Brid.) Lisa.

Materials and Methods

All available types and numerous collections of *Didymodon* sect. *Fallaces* from Europe, Africa, North America, and Asia have been studied. This revision is based on 1130 specimens deposited in the following institutional and personal herbaria: B, BCB, BM, BP, BR, C, CAIA, CAME, CANM, CGE, CLU, COI, DUKE, E, FCO, FI, G, GB, GDA, GJO, GZU, H, HBG, IRAN, JE, L, LE, LISU, M, MA, MO, MUB, NMW, NY, O, PAMP, PC, PO, PRC, RO, S, SINU, SOM, VAL, VIT, W, WB, WU, Z, herbarium T. L. Blockeel (Sheffield, United Kingdom), herbarium A. Cogoni (Cagliari, Italy), herbarium R. Düll (Bad Münstereifel, Germany), herbarium W. Frey (Berlin, Germany), herbarium J. Martínez-Abaigar (Logroño, Spain), herbarium R. B. Pierrot (Dolus d'Oléron, France), herbarium M. Sabovljevic (Belgrade, Serbia, and Montenegro), herbarium R. Skrzypczak (Montbrison, France), herbarium C. C. Townsend (Twickenham, London, United Kingdom).

Specimens were examined in a 2% potassium hydroxide solution.

Leaf areolation and ornamentation was studied using a Jeol JSM-6100 SEM at the University of Murcia. The material was fixed in 3% glutaraldehyde with 0.1M cacodylate buffer at 4°C, washed in cacodylate and saccharose buffer, dehydrated in an increasing acetone gradient (30%, 50%, 70%, 90%, 100%), critical-point dried, and sputtered with a gold layer 200–300 Å thick.

World distributions are provided; major political divisions for countries are included when the information was available.

Taxonomic History

Like most of the species of *Didymodon*, those belonging to section *Fallaces* were attributed to different genera (*Trichostomum* Bruch, *Tortula* Hedw., *Geheebia* Schimp.), although, as previously mentioned, these species were especially considered members of the genus *Barbula*. This remained the case until *Didymodon* was delimited morphologically (Saito, 1975; Zander, 1978).

The first subgeneric treatment of *Didymodon* was made by Saito (1975), who recognized two sections for the Japanese species: section *Graciles* (Milde) K. Saito and section *Didymodon*. The section *Graciles* was characterized by the rounded-triangular stem, basal margins of leaves long-decurrent, and cells of the adaxial surface of the costa linear-oblong. This section included *Didymodon giganteus*, *D. eroso-denticulatus*, and *D. rigidicaulis* (Müll. Hal.) K. Saito. Zander (1978) added five species to section *Graciles* (*Didymodon fallax*, *D. laevigatus* (Mitt.) R. H. Zander, *D. michiganensis* K. Saito, *D. leskeoides* K. Saito, and *D. tophaceus*) and expanded the characterization of this section, adding as important characters the spreading to often strongly recurved leaves when moist, unistratose upper laminal cells, and adaxial stereid band usually present. Zander (1979) found an earlier name, *Tortula* sect. *Fallaces* De Not., available at the sectional level for section *Graciles*, so he proposed the new com-

bination *Didymodon* sect. *Fallaces* and synonymized section *Graciles* with this section. Zander (1993) added another morphological character to define the section as the KOH color reaction usually reddish orange and included new species in section *Fallaces*: *Didymodon calycinus* Dixon, *D. ceratodonteus* (Müll. Hal.) Dixon, *D. constrictus* (Mitt.) K. Saito, *D. hastatus* (Mitt.) R. H. Zander, *D. inundatus* (Mitt.) Broth., *D. maximus*, *D. nigrescens* (Mitt.) K. Saito, *D. spadiceus*, *D. tomaculosus*, and *D. waymouthii* (R. Br. bis) R. H. Zander, although he did not provide the number of species worldwide. He also included, exceptionally, *D. asperifolius*, a species with quadrate or shortly rectangular cells on the adaxial surface of the costa. In an evolutionary analysis of the North American species of the genus *Didymodon*, the same author (Zander, 1998) made some changes to his previous proposals, also recognizing the section *Fallaces*, but in a broader sense. He added to this section *D. subandreaeoides* (Kindb.) R. H. Zander; a year later he included this species and *D. nigrescens*, previously considered in section *Fallaces*, in the section *Rufidulus* (Zander, 1999).

This changing situation led us to think that the infrageneric classification in *Didymodon* is difficult to assess based on morphological data. That is because there are no morphological characteristics exclusive of each section, but they are defined by a combination of several features, and often a character is shared by one or more sections.

Taxonomic Treatment

Didymodon Hedw., Sp. Musc. Frond.: 104. 1801. TYPE: *Didymodon rigidulus* Hedw. (designated by Steere (1938: 186)).

Trichostomum subg. *Zygotrichodon* Schimp., Syn. Musc. Eur. (ed. 2): 169. 1876. TYPE: *Trichostomum tophaceum* Brid.

Geheebia Schimp., Syn. Musc. Eur. (ed. 2): 233. 1876. *Barbula* subg. *Geheebia* (Schimp.) Szafr., Fl. Polska Mchy 1: 213. 1957 [1958]. TYPE: *Geheebia cataractarum* Schimp.

Dactylhymenium Cardot, Rev. Bryol. Lichénol. 36: 72. 1909. TYPE: *Dactylhymenium pringlei* Cardot.

Limneria Stirt., Trans. Bot. Soc. Edinburgh 26: 428. 1915. TYPE: *Limneria viridula* Stirt.

Prionidium Hilp., Beih. Bot. Centralbl. 50: 640. 1933. TYPE: *Prionidium setschwanicum* (Broth.) Hilp.

Our own preliminary molecular data (Werner et al., 2005) suggest that the European species of section *Fallaces* seem to be polyphyletic, but no conclusion can be reached until more data are available.

Didymodon sect. **Fallaces** (De Not.) R. H. Zander, Phytologia 44: 209. 1979. *Tortula* sect. *Fallaces* De Not., Mem. Reale Accad. Sci. Torino 40: 287. 1838. *Barbula* sect. *Fallaces* (De Not.) Steere, in Grout, Moss Fl. N. Amer. 1: 174. 1938. *Barbula* subsect. *Fallaciformes* Kindb., Eur. N. Amer. Bryin. 2: 246. 1897. TYPE: *Barbula fallax* Hedw.

Didymodon sect. *Graciles* (Milde) K. Saito, J. Hattori Bot. Lab. 39: 501. 1975. *Barbula* sect. *Graciles* Milde, Bryol. Siles., 117. 1869. TYPE: *Barbula rigidicaulis* K. Saito.

The species of section *Fallaces* share the following combination of characters: ovate, ovate-lanceolate, or lanceolate leaves (lingulate in *Didymodon tophaceus*) that are erect-patent to squarrose when moist, generally keeled; lamina unistratose, orange to dark red with KOH (*D. maschalogena* sometimes yellowish), margins weakly to strongly decurrent, plane or recurved from base to ¾ of the leaf, unistratose, not apiculate; costa ending below the apex or percurrent (shortly excurrent in *D. tomaculosus*), ventral cells of the costa in upper leaf elongated (quadrate or shortly rectangular in *D. asperifolius* and *D. tomaculosus*), with generally one layer of guide cells, generally with ventral stereids; upper and middle laminal cells without papillae or with one to three simple or bifurcate papillae per cell; peristome well developed, with straight or spirally twisted teeth.

Key to Species of *Didymodon* sect. *Fallaces* in Europe, North Africa, Macaronesia, and Southwest and Central Asia

1a. Plants with rhizoidal tubers or gemmae in the leaf axils.
  2a. Plants with rhizoidal tubers but not gemmae; stems without central strand or weakly differentiated; leaves incurved or spirally twisted, appressed to erect-patent when dry; costa shortly excurrent or percurrent . . . . . 8. *D. tomaculosus*
  2b. Plants with gemmae in the leaf axils, but not rhizoidal tubers; stems with central strand clearly differentiated; leaves catenulate when dry; costa ending below the apex or percurrent . . . . . 5. *D. maschalogena*
1b. Plants lacking both rhizoidal tubers or gemmae in the leaf axils.
  3a. Ventral cells of the costa in upper leaf shortly rectangular to quadrate . . . 1. *D. asperifolius*
  3b. Ventral cells of the costa in upper leaf elongated.
    4a. Leaves lingulate to oblong-lanceolate, with obtuse or rounded apex; costa generally ending several cells below the apex, very rarely percurrent . . . . . 9. *D. tophaceus*
    4b. Leaves lanceolate, with apex generally

acute (obtuse in *D. spadiceus*); costa ending at the apex or just below the apex.

5a. Leaves strongly recurved to squarrose when moist.
  6a. Plants generally to 3 cm high; upper leaves generally to 2 mm long; transverse section of the costa with 2 to 3 guide cells, without ventral stereids . . . . . 3. *D. ferrugineus*
  6b. Plants generally more than 3 cm high; upper leaves more than 2 mm long; transverse section of the costa with (3 to)4 to 8(to 9) guide cells, with 1 to 3 layers of ventral stereids . . . . . 6. *D. maximus*
5b. Leaves erect-patent to spreading, very rarely slightly recurved when moist.
  7a. Plants generally more than 4 cm high; leaves undulate when moist; upper and middle laminal cells strongly sinuous, basal cells pitted . . . 4. *D. giganteus*
  7b. Plants to 4 cm high; leaves not undulate when moist; upper and middle laminal cells not or very slightly sinuous; basal cells not pitted.
    8a. Leaf apex acute; margins recurved from base to ½ or ¾; transverse section of the costa with (2 to)3 to 5(to 6) guide cells; peristome spirally twisted, more than 400–1300(1700) µm long . . . . . 2. *D. fallax*
    8b. Leaf apex generally obtuse; margins recurved in the lower half; transverse section of the costa with (4 to)5 to 9(to 10) guide cells; peristome straight, generally less than (100)135–450(650) µm long . . . . . 7. *D. spadiceus*

1. Didymodon asperifolius (Mitt.) H. A. Crum, Steere & L. E. Anderson, Bryologist 67: 163. 1964. *Barbula asperifolia* Mitt., J. Linn. Soc., Bot. Suppl. 1: 34. 1859. TYPE: [India.] "Sikkim, Momay, Regio alp., 15,000 ft.," *J. D. Hooker s.n.* (lectotype, designated by Li et al. (2001: 157), NY not seen; isotype, BM!). Figure 2A–E.

Didymodon rufus Lorentz, Bryoth. Eur.: 621. 1863. TYPE: [Austria.] "In Carinthiae alpe Pasterze," 1861, *P. G. Lorentz s.n.* (lectotype, designated here, RO!; isotype, PC!).

Barbula sinensi-fallax Müll. Hal., Nuovo Giorn. Bot. Ital. 3: 100. 1896. TYPE: "China interior, provincia Schen-si sept., in monte Thae-pei-san," Aug. 1894, *J. Giraldi s.n.* (lectotype, designated here, FI!).

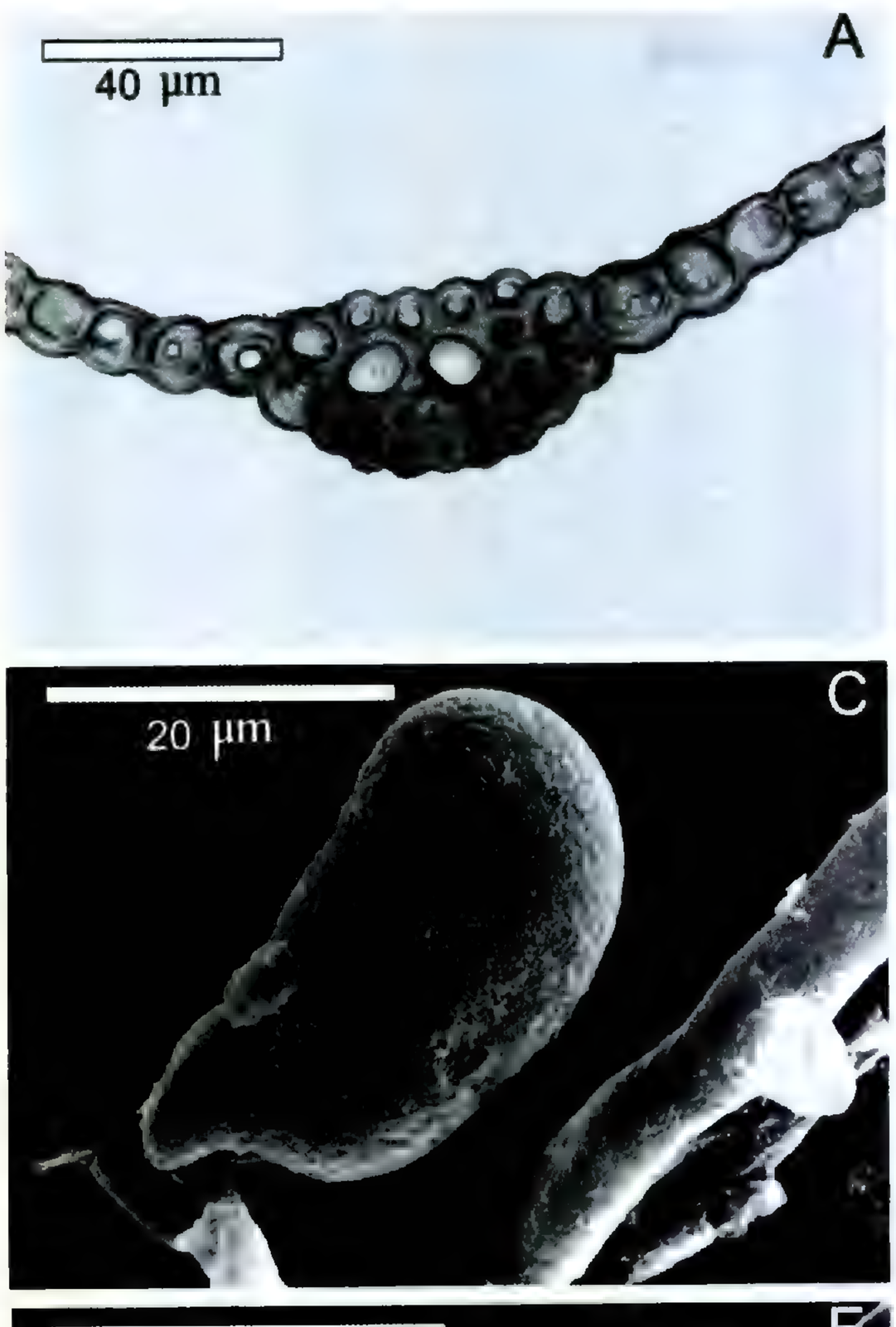
Barbula kneuckeri Loeske & Osterwald, Verh. Bot. Vereins Prov. Brandenburg 49: 45. 1907. TYPE: [Germany.] "Allgäuer, Nebelhorn, 2200 m," 17 Aug. 1904, *J. A. Kneucker s.n.* (lectotype, designated here, HBG!).

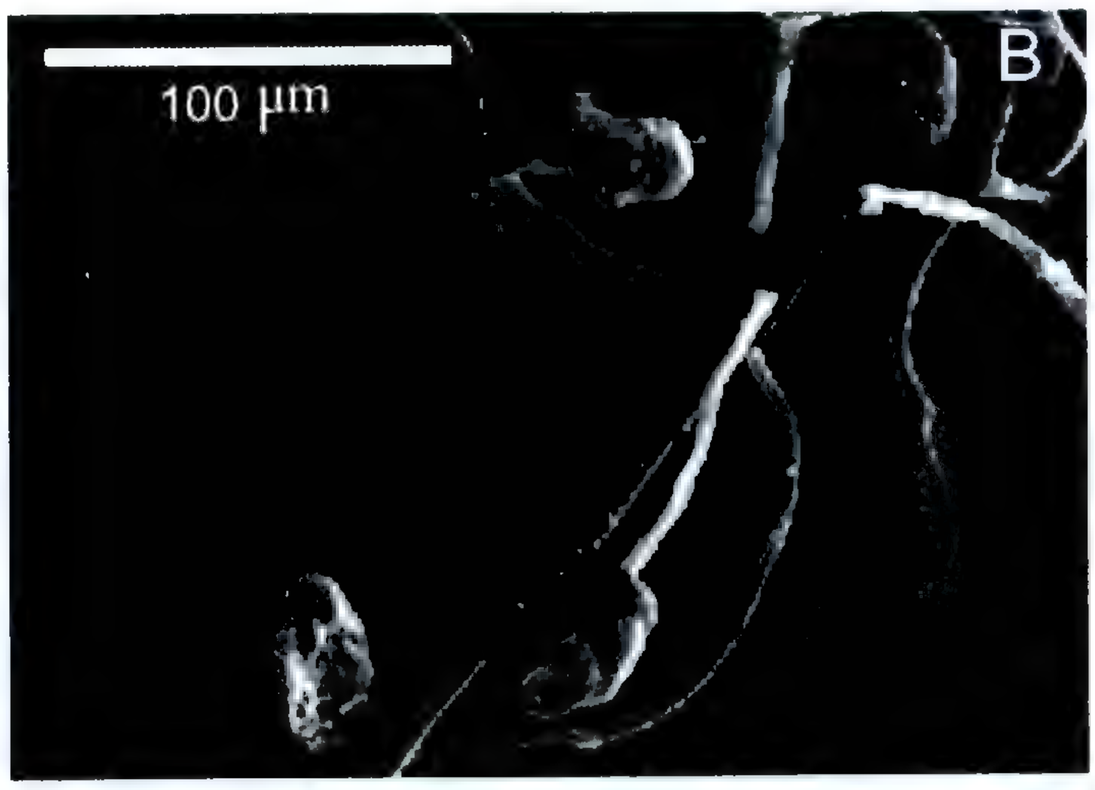
Plants 1–5 cm high, growing in loose or dense turfs, brown-reddish; *stems* erect or ± decumbent, simple or branched, without central strand; *rhizoidal tubers* absent. *Leaves* appressed to erect-patent when dry, only the upper leaves slightly twisted, recurved to squarrose, more rarely patent to spreading, not undulate when moist, ovate to ovate-lanceolate, gradually narrowed to the apex, keeled, decurrent at base, 1.3–3 × 0.5–0.95 mm; lamina unistratose, dark red with KOH stain; apex acute; margins entire, sometimes papillose-crenulate, recurved from base to near the apex, sometimes to ⅔ of the leaf; *costa* 35–75 µm wide at leaf base, ending below the apex or percurrent, ventral cells of the costa in upper leaf shortly rectangular to quadrate, papillose, dorsal cells of the costa in upper leaf quadrate, smooth or papillose, in transverse section at leaf base circular, with 2 to 4(to 5) guide cells in 1 layer, 1(to 2) layer of ventral stereids, 1 to 2(to 3) layers of dorsal stereids, ventral epidermis strongly differentiated, papillose, dorsal epidermis differentiated, papillose; *upper and middle laminal cells* rounded, subquadrate or hexagonal, generally oblate, not sinuous, (3–)5–12.5 × 5–14 µm, with 1(to 2) simple, tall papillae per cell (sometimes low), thick-walled, collenchymatous; *basal cells* rectangular, quadrate at margins, not sinuous, (10–)15–60(–70) × (2.5–)5–12 µm, forming a ± differentiated area, smooth, thick-walled, not pitted. *Gemmae* in the leaf axils absent. *Dioicous. Sporophyte* not seen.

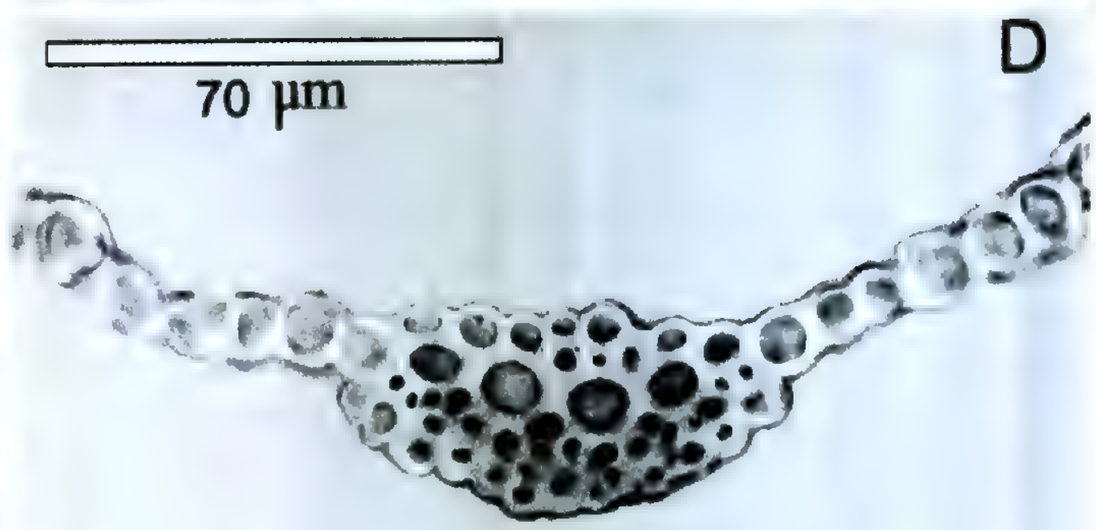
Habitat and distribution. Granite or calcareous rocks and edges of streams in alpine belt; 2300–3800 m; Africa (O'Shea, 2003), North America, temperate and tropical Asia, Europe. Reported for the first time from the Caucasus.

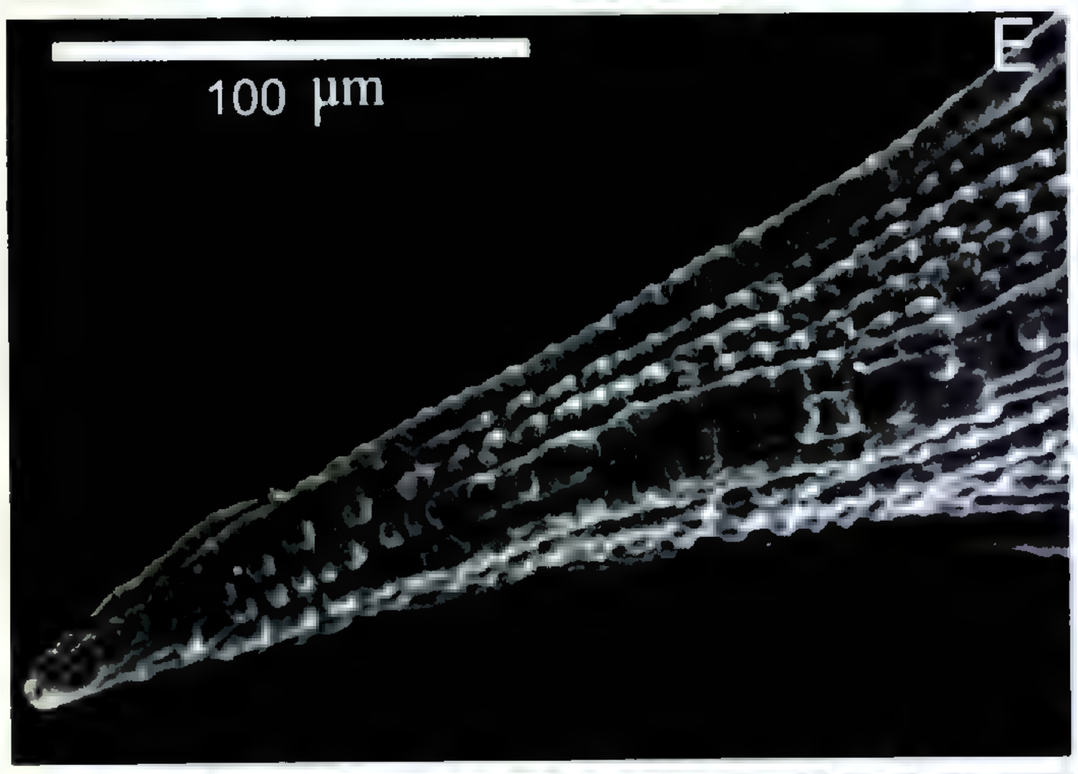
Discussion. Lorentz published his *Didymodon rufus* in number 621 of *Bryotheca Europaea von Rabenhorst.* We were unable to find any syntype of this exsiccata in B, where the original herbarium of Lorentz is deposited. We did find syntypes in RO and PC. We select as lectotype the syntype kept at RO because it is better preserved.

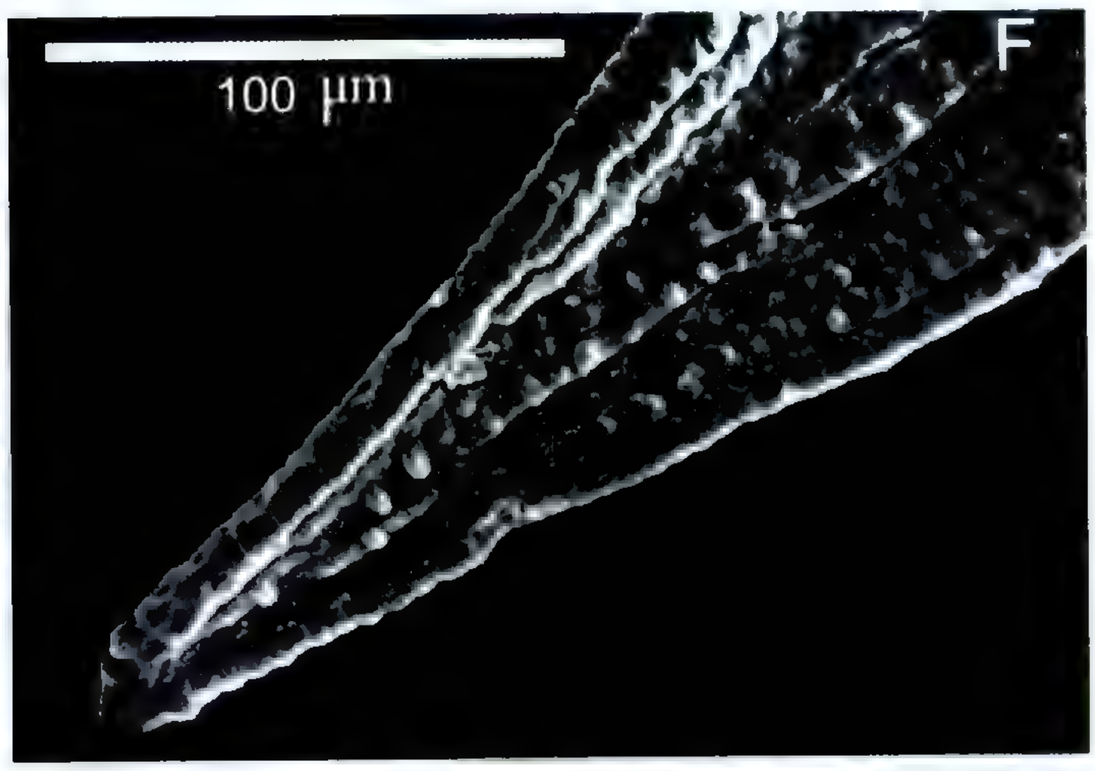
Barbula sinensi-fallax was described by Müller (1896) from material collected by Giraldi: "Ad latera montis Thae-pei-san." Müller's herbarium was deposited at B, but was destroyed in World War II. However, we detected a syntype in Levier's herbar-

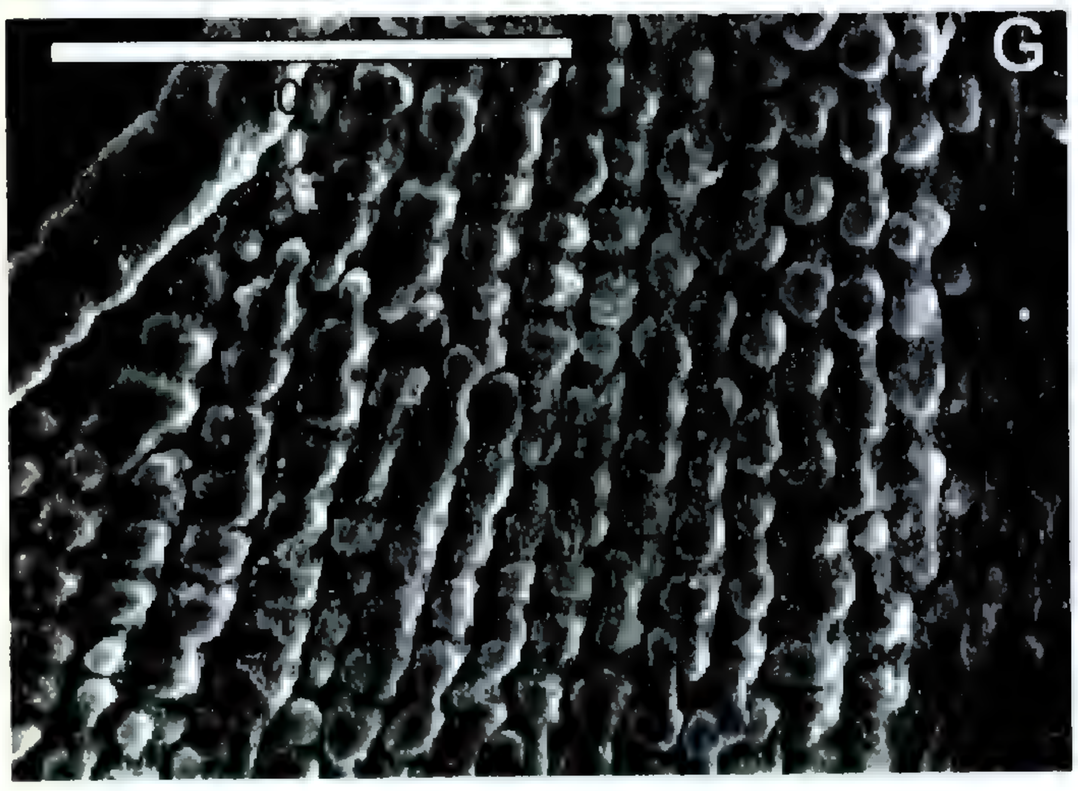












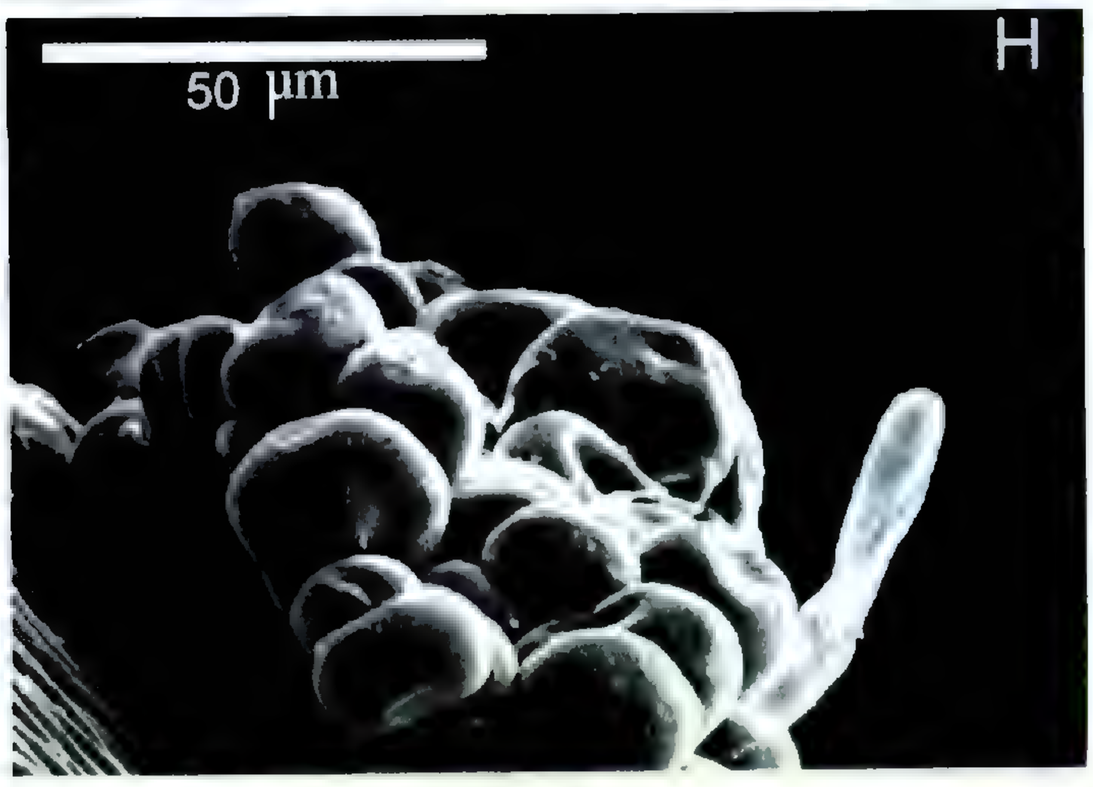


Figure 1. A–C, *Didymodon tomaculosus* (*Blockeel & Porley*, Hb. Blockeel 31/418). —A. Transverse section of the costa at leaf base. —B. Rhizoidal tubers. —C. Detail of a rhizoidal tuber. D–H, *Didymodon maschalogena* (IRAN 4308). —D. Transverse section of the costa at leaf base. —E. Dorsal surface of leaf apex. —F. Ventral surface of leaf apex. —G. Upper laminal cells. —H. Group of gemmae in the axil of the leaf. Micrographs: A, D: LM; B, C, E–H: SEM.

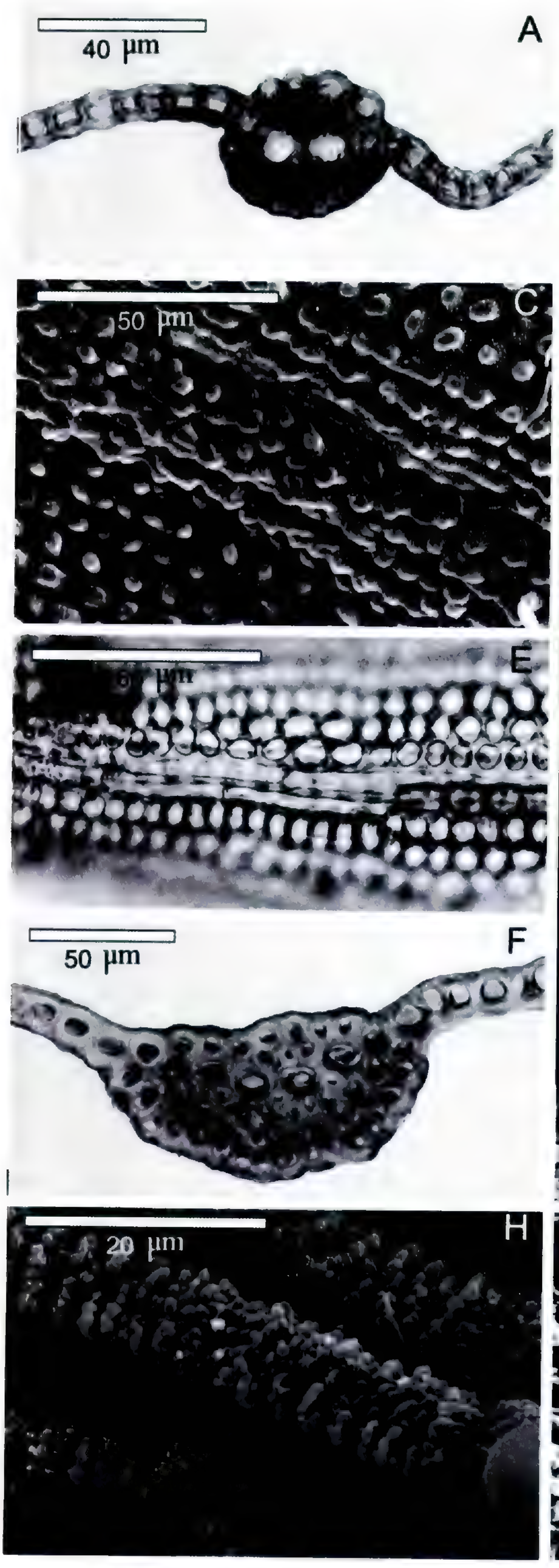
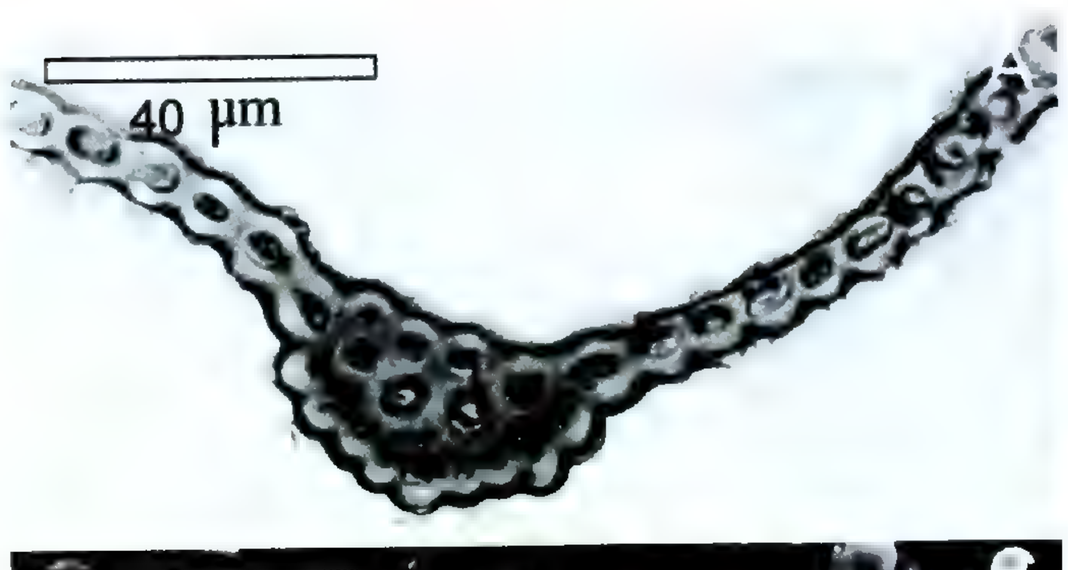
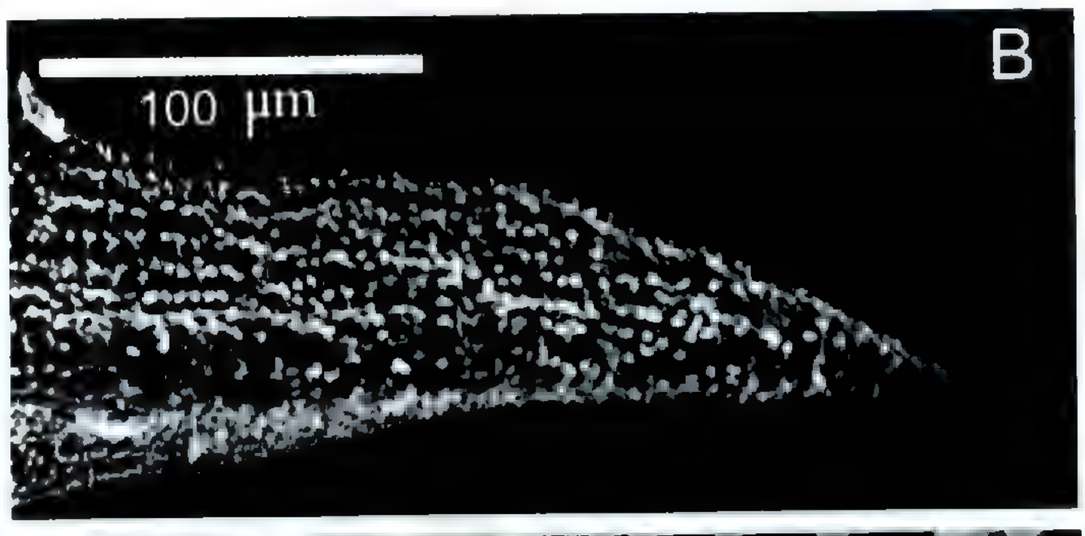
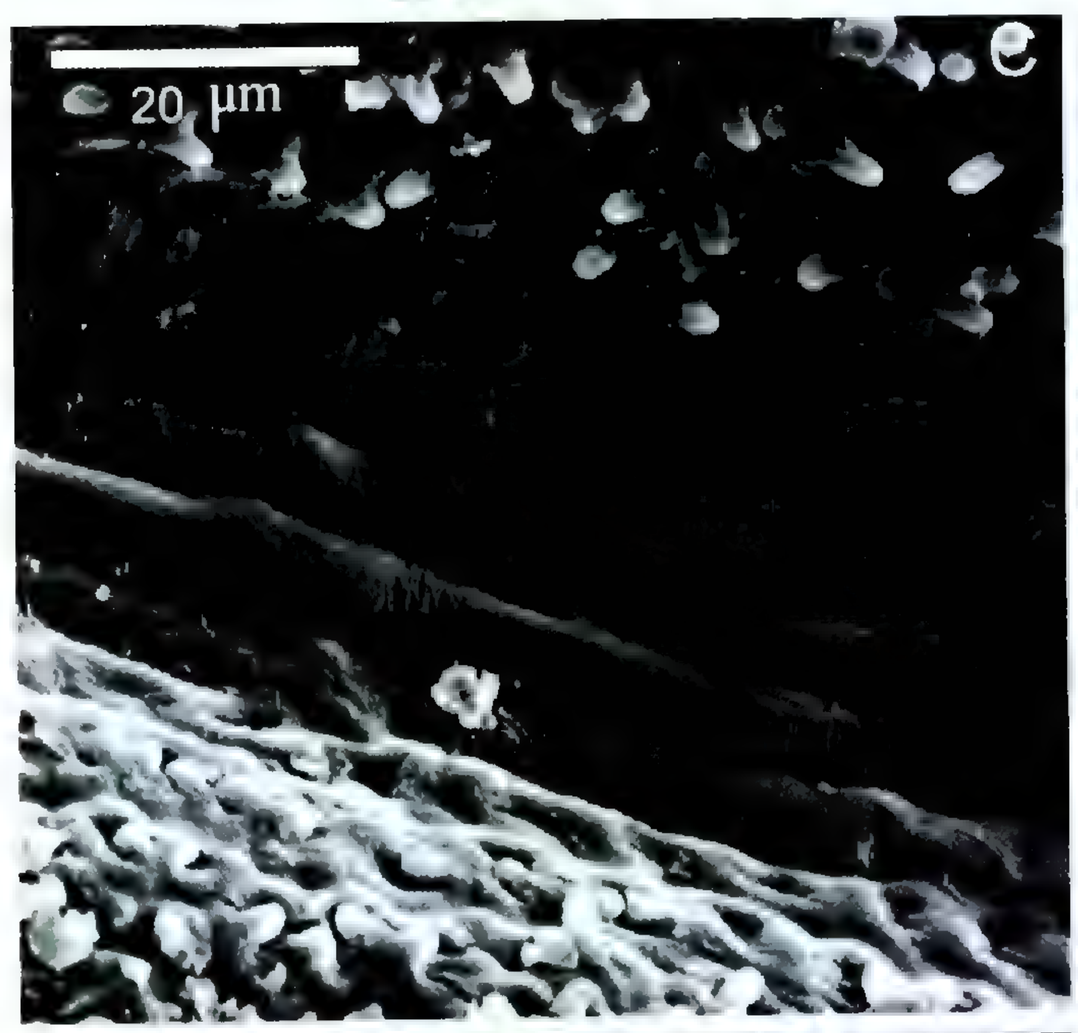
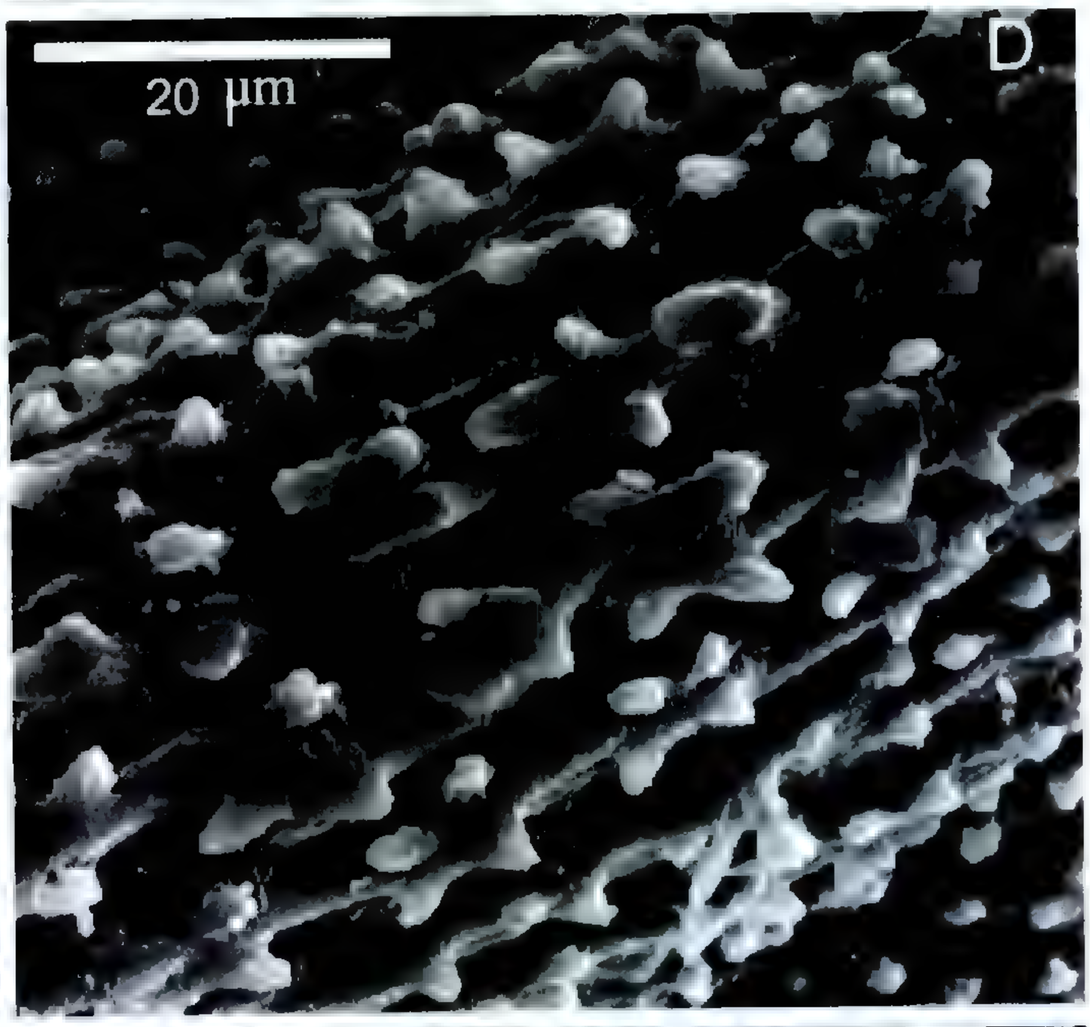


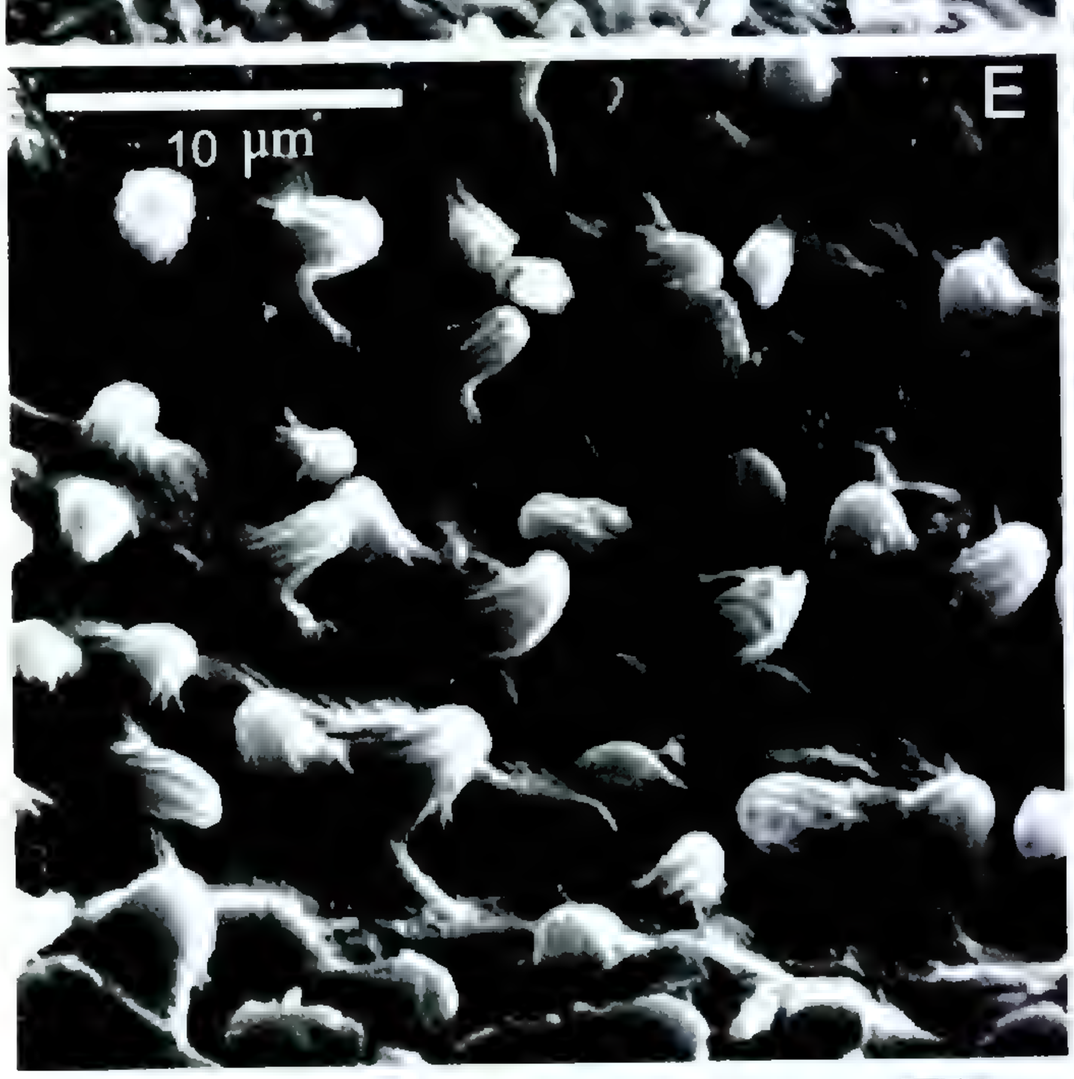
Figure 2. A–E, *Didymodon asperifolius* (*Wallace s.n.*, E). —A. Transverse section of the costa at leaf base. —B. Leaf apex. —C. Ventral surface of the costa in upper leaf. —D. Upper laminal cells. —E. Small band of elongated cells below the apex. F–I, *Didymodon tophaceus* (*Cano et al. s.n.*, MUB 11939). —F. Transverse section of the costa at leaf base. —G. Peristome. —H. Detail of the teeth peristome. —I. Ventral cells of the costa in upper leaf. Micrographs: A, E, F: LM; B–D, G–I: SEM.

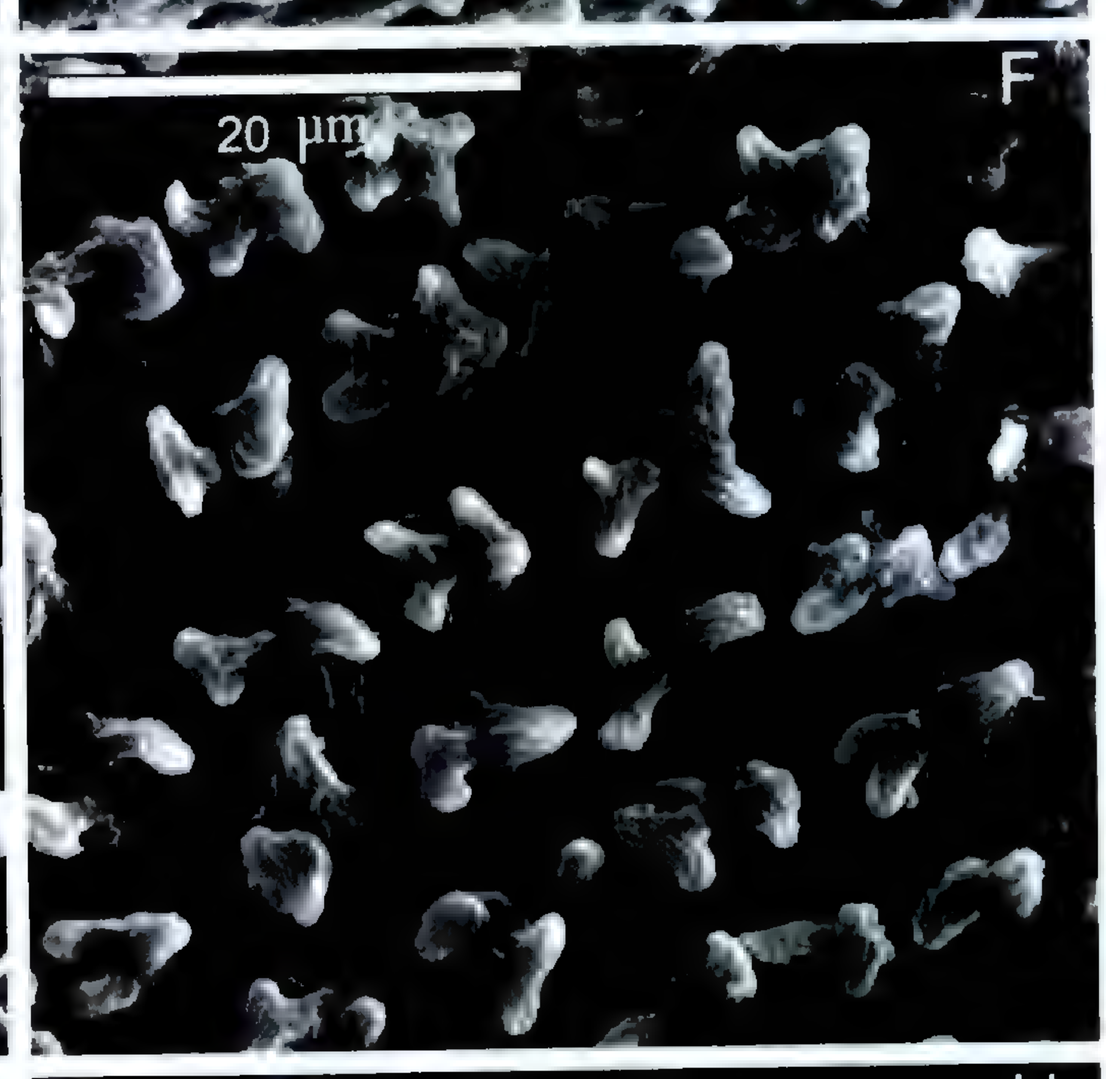


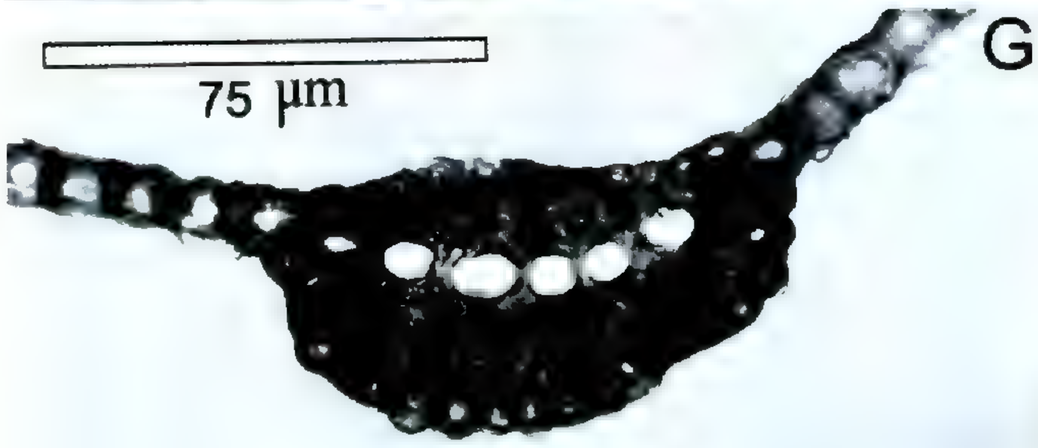












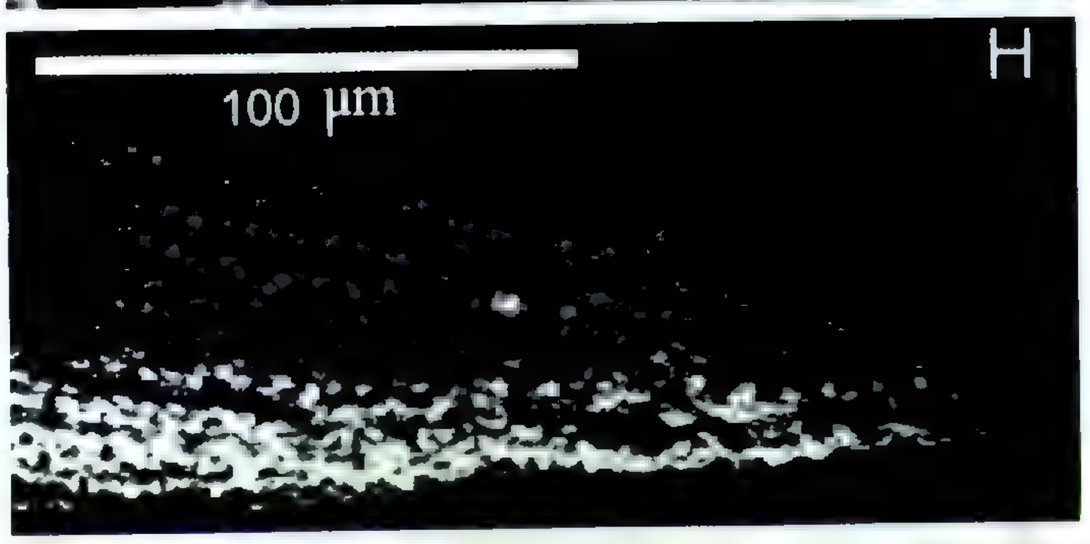
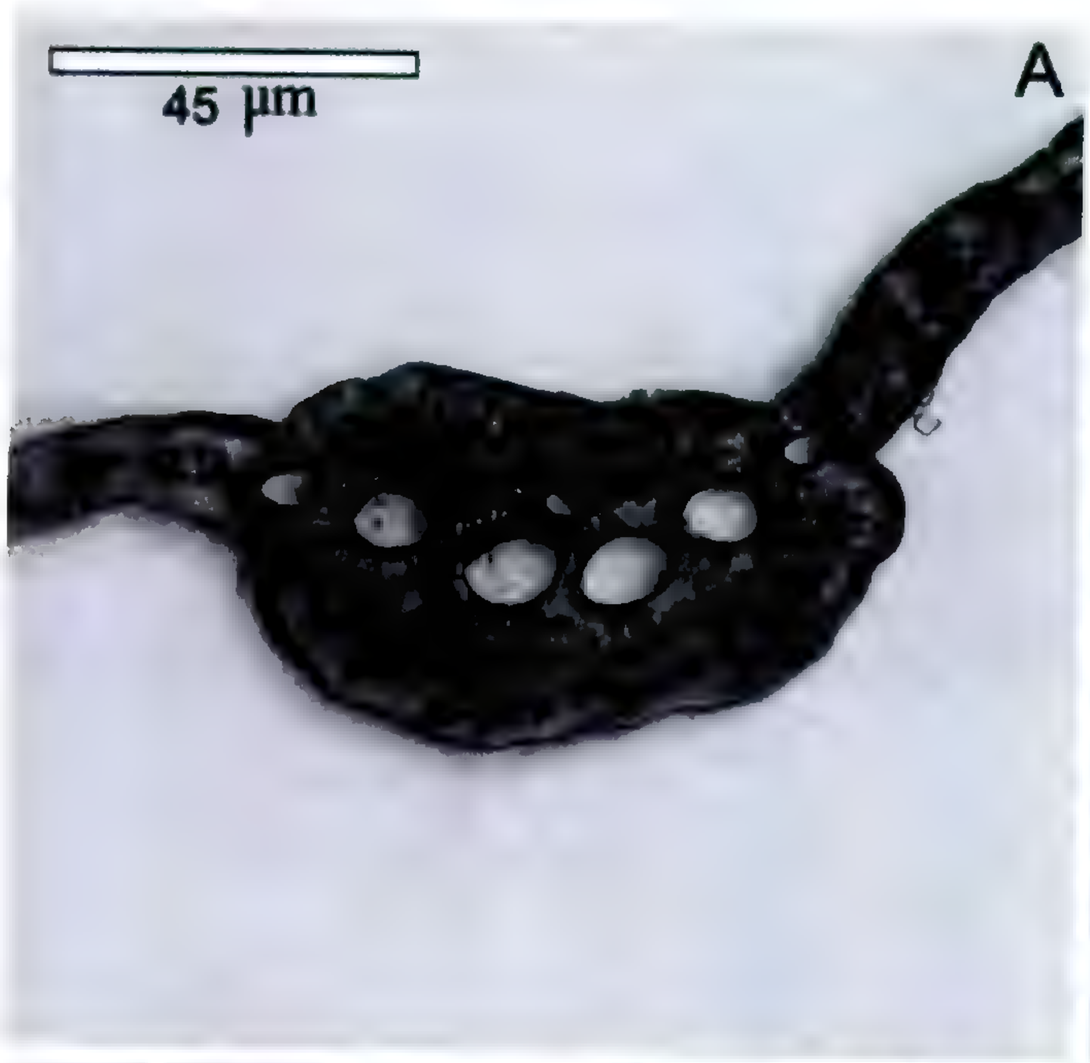
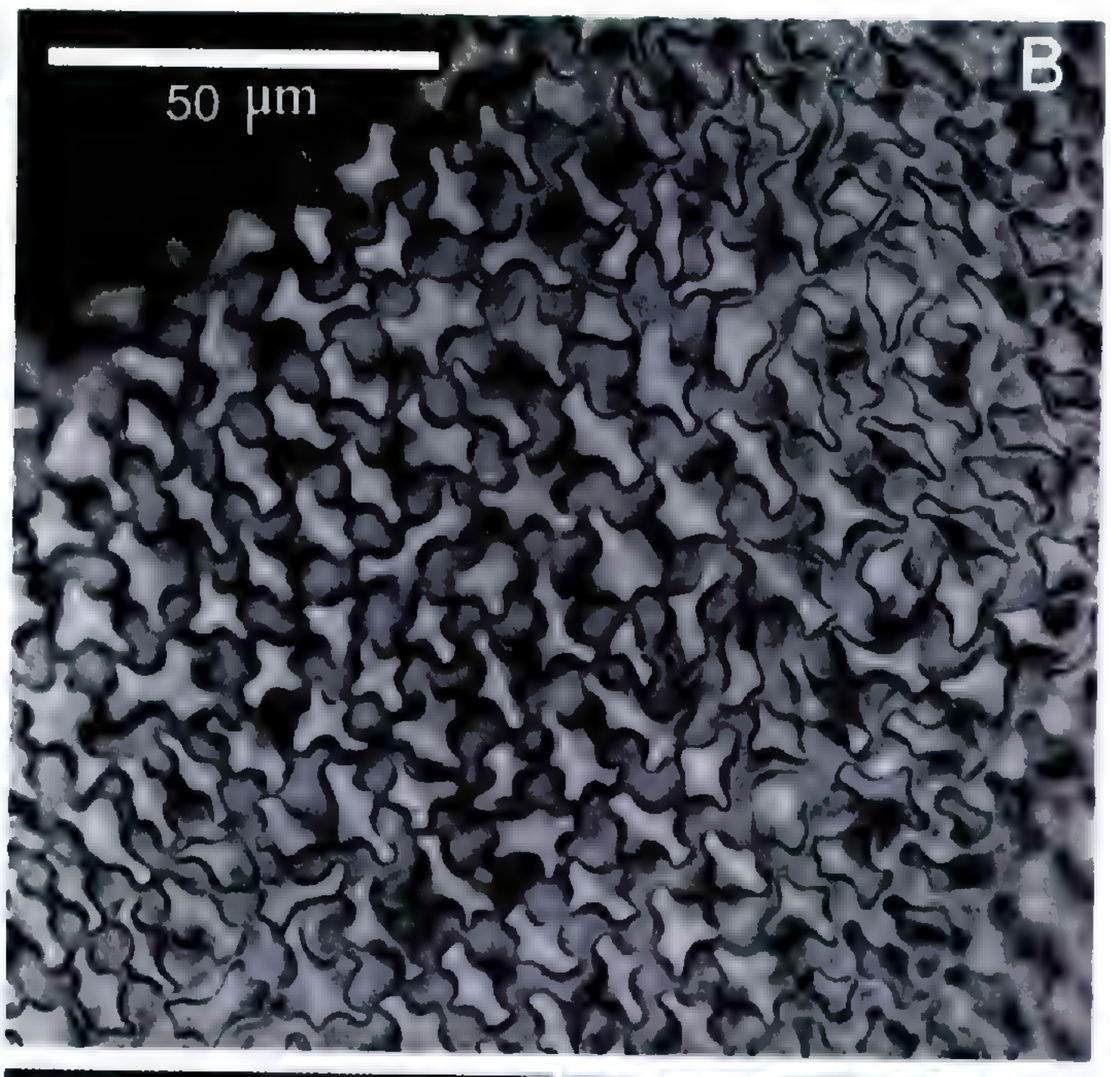
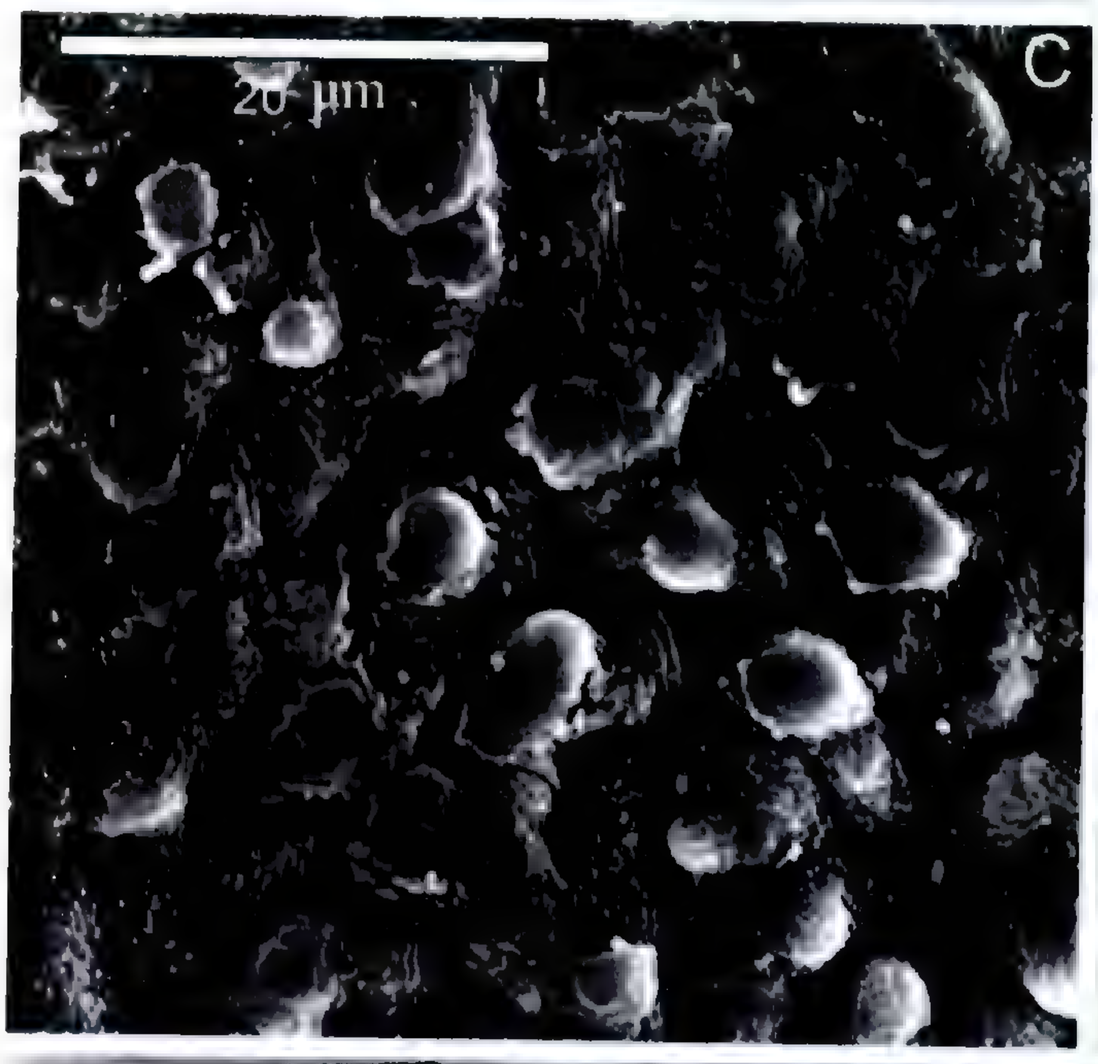
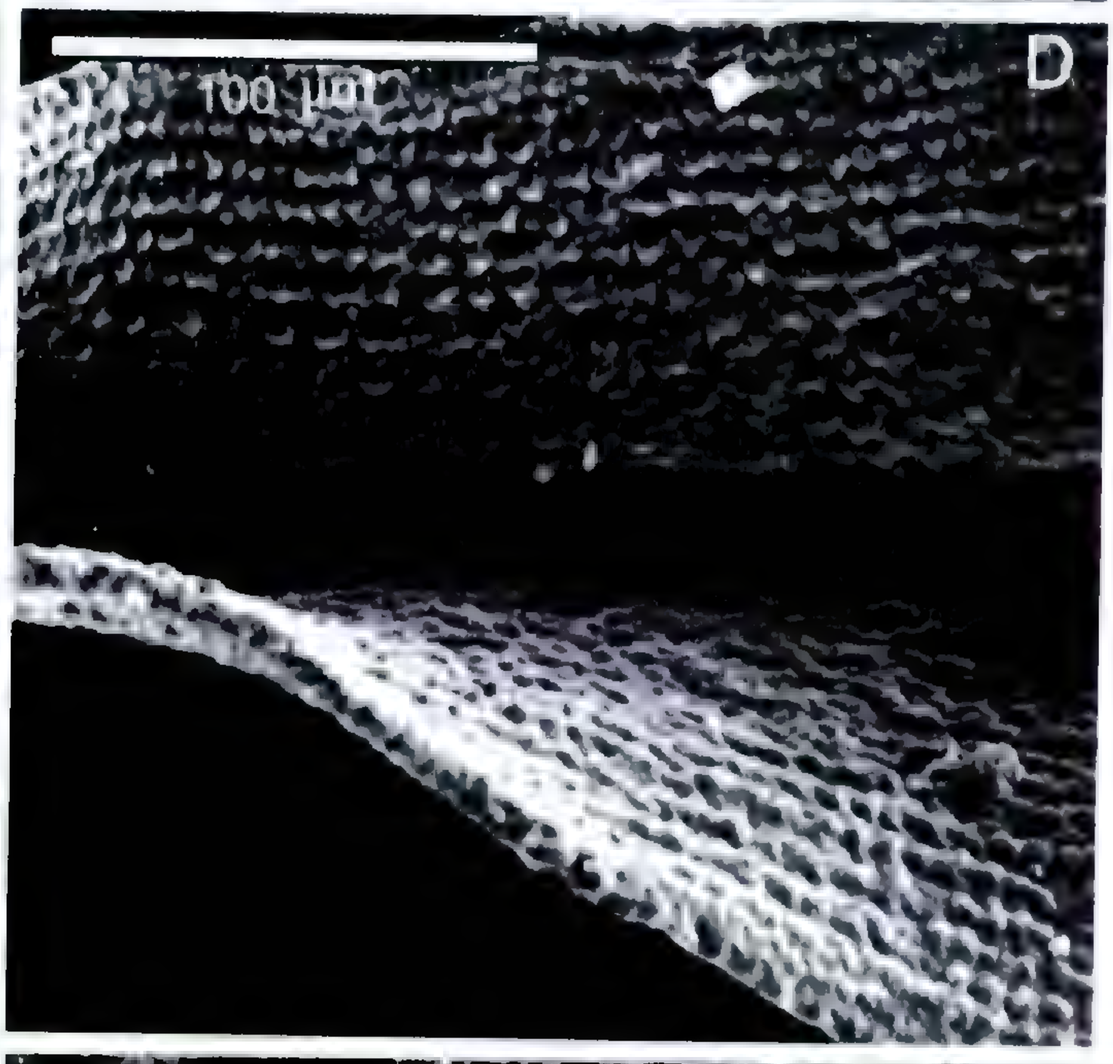


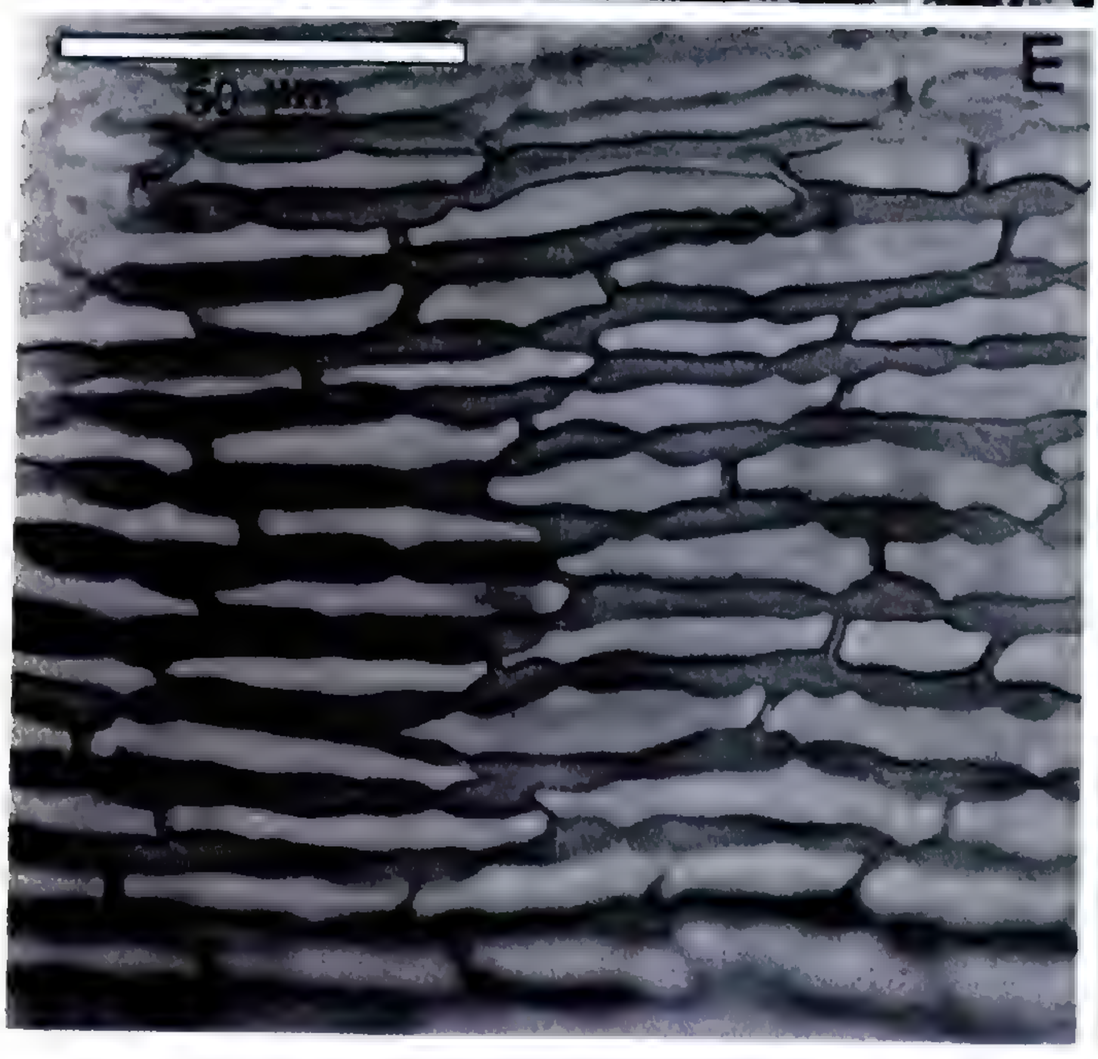
Figure 3. A–E, *Didymodon ferrugineus* (*Cano et al. s.n.*, MUB 8491). —A. Transverse section of the costa at leaf base. —B. Leaf apex. —C. Ventral surface of the costa in upper leaf. —D. Dorsal surface of the costa in upper leaf. —E. Upper laminal cells. F–H, *Didymodon maximus* (*Long 14626*, E). —F. Upper laminal cells. —G. Transverse section of the costa at leaf base. —H. Leaf apex. Micrographs: A, G: LM; B–F, H: SEM.











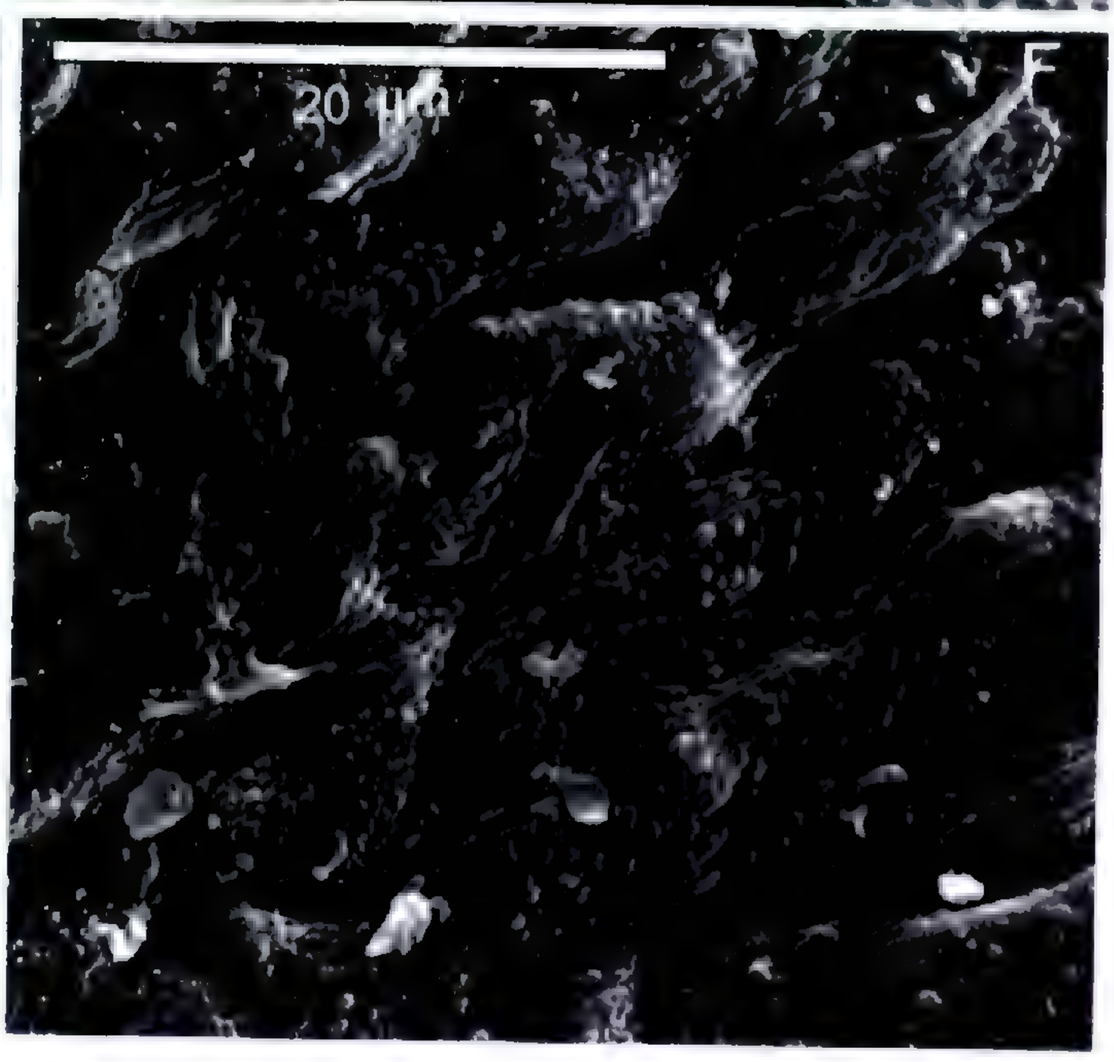


Figure 4. A–F, *Didymodon giganteus* (*Artaria s.n.*, BM). —A. Transverse section of the costa at leaf base. —B, C. Upper laminal cells. —D. Ventral surface of the costa in upper leaf. —E, F. Basal cells. Micrographs: A, B, E: LM; C, D, F: SEM.

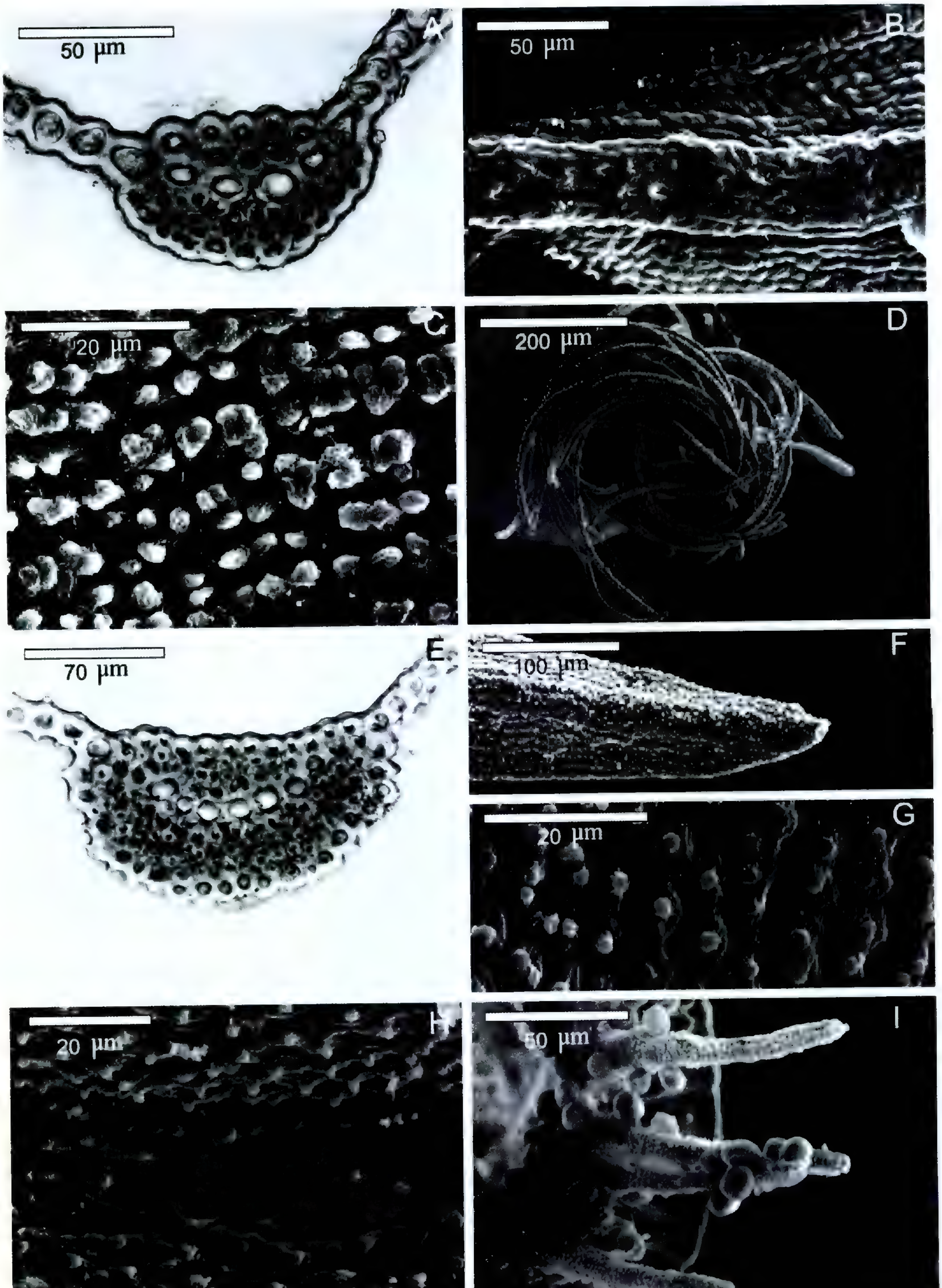


Figure 5. A–D, *Didymodon fallax* (*Ros s.n.*, MUB 13461). —A. Transverse section of the costa at leaf base. —B. Dorsal surface of the costa and laminal cells in upper leaf. —C. Upper laminal cells. —D. Peristome. E–I, *Didymodon spadiceus* (*de Miguel s.n.*, PAMP 2767). —E. Transverse section of the costa at leaf base. —F. Leaf apex. —G. Upper laminal cells. —H. Ventral surface of the costa in upper leaf. —I. Peristome. Micrographs: A, E: LM; B–D, F–I: SEM.

ium at FI that matches the locality indicated in the protologue. We select this material as lectotype.

The protologue of *Barbula kneuckeri* cited two specimens from the same locality: "Nebelhorn, auf Dolomit bei 2000 m am 16 August 1904." One was collected by Kneucker and the other by the authors of the species. Loeske and Osterwald's collections at B were also lost in World War II. A search in the two herbaria where Kneucker's herbarium is kept (KR, H) was unsuccessful. We found a specimen collected by Kneucker at HBG, which totally agrees with the protologue, and we select this latter specimen as lectotype of *Barbula kneuckeri*.

Didymodon asperifolius has an Arctic-Alpine distribution and is uncommon in the area studied, where it is restricted to high mountain ranges (Alps, Pyrenees, Caucasus, Turkistan). *Didymodon asperifolius* shares numerous characters with *D. ferrugineus*, e.g., the shape and disposition of the leaves when moist, apex shape, costa thickness, shape and size of the leaf cells, and color of the lamina with KOH. However, the two species are easily distinguished because *D. ferrugineus* has elongated cells in the upper half of the ventral costa, while in *D. asperifolius* these are quadrate or shortly rectangular. It is important not to confuse this feature with a small band of elongated and translucent cells just below the apex, which most specimens of *D. asperifolius* have. In addition, *D. asperifolius* shows 1(to 2) simple papillae per cell, while *D. ferrugineus* has (1 to)2 to 4 simple or bifurcated papillae.

No central strand was observed in any of the specimens studied although, according to Zander (1978), they may have such a feature.

Selected specimens examined. KAZAKSTAN. **Alma Ata:** Tianschan Septentrionalis, Montes Transilienses, superior pars vallis Malaja Almaatinka, prope glaciem Tujok-Su, *Lisowski s.n.* (BP 107038). AUSTRIA. **Kärnten:** in Alpe "Fasihaunernik," prope Malta, *Breidler s.n.* (BM). **Steiermark:** Kuppe des Sinabell im Dachsteingebirge bei Schladming, *Baumgartner s.n.* (MO). **Tirol:** Zaythal, Sulden, *Nicholson & Dixon s.n.* (MO). FRANCE. **Savoie:** Col du Petit Mont, Cenis, *Wallace s.n.* (E). ITALY. **Lombardia:** Monte Gavio, *Möller s.n.* (S). **Trentino-Alto Adige:** Tirol, Brenner, *Warnstorf s.n.* (RO). **Valle d'Aosta:** Gressoney-Saint Jean, dalla cima del Grauhaupt, *Carestia s.n.* (RO). RUSSIA. **North Ossetia:** N Ossetian Nature Reserve, upper course of Tsej River, *Abramova s.n.* (SINU). **Dagestan:** Tlyarskij, *Onipchenko s.n.* (SINU). **Karachaevo-Cherkessia:** Malokarachaevsk, Tokhana Gorge, Khudes River upper course, *Onipchenko 30/02* (SINU). SPAIN. **Lérida:** Alta Ribagorca, entre els pics de Coma-lo-Forno i Besiberri Sud, *Ballesteros s.n.* (BCB 28654). SWITZERLAND. **Bern:** Südabhang des Niesen, *Culmann s.n.* (GJO). **Graubünden:** Davos, Rhaetia, *Amann s.n.* (Z). **Valais:** sur La Cabane Britannia, *Amann s.n.* (Z); Südabhang des Saretschpasses, *Culmann s.n.* (Z). CANADA. **Quebec:** Mingan Archipelago Nat. Park Reserve, Ile Nue de Mingan, *Hedderson 8624* (DUKE).

2. **Didymodon fallax** (Hedw.) R. H. Zander, Phytologia 41: 28. 1978. *Barbula fallax* Hedw., Sp. Musc. Frond. 120. 1801. *Bryum fallax* (Hedw.) Dicks. ex With., Syst. Arr. Brit. Pl. (ed. 4) 3: 816. 1801. *Tortula fallax* (Hedw.) Schrad. ex Turner, Muscol. Hibern. Spic. 48. 1804. TYPE: locality not indicated, "Chemnitis lecta" (lectotype, designated by Zander (1978: 28), G!). Figure 5A–D.

Trichostomum rigidulum var. *paludosa* M. T. Lange, Bot. Tidsskr. 3: 20. 1869. Syn. nov. TYPE: [Denmark.] "Vejle Fjord," Aug. 1867 (lectotype, designated here, C!).

Barbula adriatica Baumgartner, Denkschr. Kaiserl. Akad. Wiss., Wien. Math.-Naturwiss. Kl. 92: 325. 1916. TYPE: [Croatia.] "Dalmatien, Insel Lissa, zw. Lissa und Comisa, 50–100 m," 4 Apr. 1910, *J. Baumgartner s.n.* (lectotype, designated here, W!; isotypes, L!, MA!, S!).

Plants 0.3–2.8 cm high, growing in dense or loose turfs, olive-green or brown; *stems* erect, simple or branched, central strand differentiated; *rhizoidal tubers* absent. *Leaves* appressed to erect-patent, incurved when dry, sometimes slightly spirally twisted, erect-patent, spreading or slightly recurved, not undulate when moist, lanceolate to ovate-lanceolate, sometimes keeled, decurrent at base, usually with 2 small plicae at base, 0.6–2.5 × 0.2–0.8 mm; lamina unistratose, reddish orange, rarely yellowish green with KOH stain; apex acute; margins entire, recurved from base to ½ or ¾ of the leaf, sometimes almost plane; *costa* 30–120(–140) μm wide at leaf base, percurrent, ventral cells of the costa in upper leaf elongated, smooth, dorsal cells of the costa in upper leaf shortly quadrate to rectangular, smooth or papillose, in transverse section at leaf base semicircular, with (2 to)3 to 5(to 6) guide cells in 1 layer, (0 to)1 to 2 layers of ventral stereids, (0 to)1 to 3 layers of dorsal stereids, with or without ventral epidermis, smooth, dorsal epidermis differentiated, rarely undifferentiated, smooth or papillose; *upper and middle laminal cells* rounded to hexagonal, oblate or not, not sinuous, (4–)5–15(–18) × (4–)5–13(–17) μm, smooth or with 1 to 3 simple or bifurcate papillae per cell, thick-walled, collenchymatous; *basal cells* rectangular or subquadrate, not sinuous, (7–)10–40(–50) × 5–12.5 μm, smooth, generally thick-walled, not pitted. *Gemmae* in the leaf axils absent. *Dioicous. Seta* erect, 0.7–2.3(–2.7) cm long, reddish brown, spirally twisted to left throughout; *capsule* erect or slightly inclined, cylindrical to ellipsoid, 1.1–2.6 × 0.39–0.7 mm, brown; *peristome* of 16 teeth cleft to

near base, filiform, papillose, spirally twisted to the left, 400–1300(–1700) μm long, yellowish brown to reddish brown; *operculum* long conical, 0.9–1.5 mm long; *calyptra* cucullate, 2.4–2.8 mm. *Spores* spherical, 7–12.5 μm diam., weakly papillose, brown-yellowish or yellowish green.

Habitat and distribution. On basic soil (calcareous, clayey, sandy, or nitrified) generally open, more rarely on saline soil, edges of paths, on calcareous and dolomite rocks, fissures or artificial walls; 0–1950 m; Africa, North America (Zander, 2002), South America (Churchill et al., 2000), temperate Asia, Europe.

Discussion. The protologue of *Trichostomum rigidulum* var. *paludosa* includes "Ibaek ved Veile af J. Lange." In C, we found a sheet from Lange's herbarium, the label of which matches the locality and collector of the only specimen mentioned in the protologue. We here select this specimen as lectotype. After examinig the type material, we conclude that there are no morphological differences between this taxon and *Didymodon fallax*.

The protologue of *Barbula adriatica* includes: "Sant' Andrea: zwischen Bimbul und Cote 311 m. bei Zankić, 9/VI.1911." Furthermore, the author mentioned that he had collected this species previously from several places in Istria and Dalmatia. We examined Baumgartner's herbarium at W, but we did not find any specimen with a label that showed the first locality mentioned in the protologue. However, we found in this herbarium one specimen collected by Baumgartner from Dalmatia in 1910, which is selected as lectotype.

Didymodon fallax is frequently confused with other species in the genus not belonging to section *Fallaces*, especially *D. acutus* (Brid.) K. Saito, because the band of elongated cells on the ventral side of the costa in the upper half of the leaf may be quite small and not clearly distinguishable. It may also be confused with *Ceratodon purpureus* (Hedw.) Brid., which, like the genus *Didymodon*, has axillary hairs with a brown basal cell but which differs from *D. fallax* by the slightly toothed margin near the apex and by the light yellow color of the lamina with KOH. *Didymodon fallax*, on the other hand, has an entire margin, and the reaction with KOH turns the lamina typically a reddish orange or rarely yellowish green.

Selected specimens examined. ALGERIA. **Algiers:** Route de la Mouzaia, *Tixier 6477* (PC). **Blidah:** Blidah, *Graef s.n.* (JE). **Jijel:** Bosque Texenna, *Ros s.n.* (MUB 13147). **Mestghamen:** de Mostaganem a Cap Ivi, *Ros s.n.* (MUB 13146). **Oran:** St. Eugène, *Appert s.n.* (JE). **Relizane:** Oued Rhiou, *Ros s.n.* (MUB 13141). EGYPT. **Fayum:** Manshy'iet Halpha, *Shabbara 105/86* (CAIA). MOROCCO. **Meknès-Tafilalt:** de Ifrane a Azrou km 9, *Ros s.n.* (MUB 13454). **Oriental:** Nador, *Ros s.n.* (MUB 13461). **Tanger-Tétouan:** El-Fendek, prop de Tetuan, *Brugués s.n.* (BCB 31714). **Taza-Al Hoceima-Taounate:** Jbel Bouhalla, *Cano et al. s.n.* (MUB 10566). TUNISIA. Kerkouane, *Ros s.n.* (MUB 12512); Djebel Zaghouan, *Poelt 6318* (GZU). GEORGIA. Dzhava, upper course of Liakhvi River, *Dombrovskaya s.n.* (SINU). **South Ossetia Autonomous Oblast:** inter pp. Dzaw et Raro, *Woronow 957* (LE). JORDAN. **Irbid:** Ajlun, Eshtafarineh, *El-Oqlah s.n.* (Hb. Frey 1–4314F, Germany); Jerash, King Talal Dam, *El-Oqlah & Lahham s.n.* (Hb. Frey 1–4312F, Germany). KAZAKHSTAN. **South Kazakh:** Tulubas, the head of Dzhabagly Creek, *Karamyschera s.n.* (LE). LEBANON. Arayeh, Nahr Beirut, *Davis s.n.* (BM, E); above the palace of Beit ed Din, ca. 28 mi. S of Beirut, *Townsend 71/196* (E). TURKEY. **Antalya:** Beymelek Koyer, ca. 20 km WSW of Finike, *Nyholm 690c/72* (S). **Aydin:** 4–5 km from Soke towards Kusadasi, *Wallace s.n.* (NMW). **Balikesir:** Paß über Sindirgi, *Walther 2396a* (HBG). **Bolu:** Abant ca. 30 km SW Bolu, *Nyholm 937/74* (S). **Isparta:** Barla Dagi, W Barlu, *Nyholm 333/72* (S). **Izmir:** ca. 10 km S Selcuk, *Nyholm 79f/72* (S). **Karaman:** Sheyhan, ca. 2 km W Osmaniye near the river Dere, *Bremer & Nyholm 190/78* (S). **Manisa:** 11 km W of Manisa, *Nyholm 1029/71* (S). **Mugla:** Icmeler, near of Marmaris, *Wallace s.n.* (NMW). **Ordu:** Vilayet Ordu, Ünye, *Rubers 4530* (L). UZBEKISTAN: Fergana, *Mafeev s.n.* (LE). ANDORRA. Santa Coloma, Popladó, *Vives s.n.* (BCB 35670). AUSTRIA. **Tirol:** bei Windisch, *Breidler s.n.* (GJO). BELGIUM. Namur, Rochefort, *Vandenbroeck s.n.* (GJO). BOSNIA HERZEGOVINA. Bistrica bei Foca, *Glowacki s.n.* (GJO); Trebevic prope Sarajevo, *Maly s.n.* (HBG). CROATIA. Ragusa, Insel Lapad, *Klofs 4331* (B); Vincural bei Pola, *Glowacki s.n.* (GJO). CYPRUS. Eastern Troodos, N slopes of Mt. Kionia, *Blockeel* (Hb. Blockeel 26/126, United Kingdom). FRANCE. **Alpes Maritimes:** Nice, *Noday s.n.* (S). **Bas-Rhin:** Elsass, Wissemburg, *Winter s.n.* (S). **Côte-d'Or:** Beaune, *Jones s.n.* (E). **Doubs:** Cirque de Consolation N of Morteau, *Touw 13163* (L). **Haute-Corse:** Bastia, Tal des Fango, *Baumgartner s.n.* (W 27254). **Hautes-Pyrénées:** Ruisseau d'Ardalos, *Spruce s.n.* (E). **Herault:** Castelnau, Jacou, *Barkman 3915* (L). **Landes:** Calcareis, *Berthoumieu s.n.* (S). **Lozère:** Florac, sources du Pecher, *Frahm s.n.* (MUB 1180). **Manche:** Cherbourg, *Corbière s.n.* (S). **Rhône:** Lyon, *Jordan s.n.* (S). **Sarthe:** Crannes, *Monguillon s.n.* (E). **Vaucluse:** Mont Serein, sous Mont. Ventoux, *Skrzypczak s.n.* (Hb. Skrzypczak 97088, France). GERMANY. **Baden-Württemberg:** Selva Negra, Oberes Enztal, cerca de Gompelscheuer, *Werner s.n.* (MUB 6168). **Bayern:** bei der Tannenberg, *Remmler s.n.* (RO). **Brandenburg:** Postdam, *Beinhardt s.n.* (RO). **Hamburg:** Hamburg, *Röll s.n.* (WB). **Hessen:** In montb. "Rhön," *Geheeb s.n.* (RO). **Sachsen:** Dölzig bei Bärwalde, *Ruthe s.n.* (RO). **Thüringen:** Jena, *Röll s.n.* (WB). GREECE. **Crete:** Chania, 8.3 km oberhalb Skinés, *Düll s.n.* (Hb. Düll). **Central Greece and Euboea:** Athens, *Hararas s.n.* (E). **Aegean Islands:** Rhodes, Mount Profitas Elias, *Townsend 71/383* (E). **Ionian Islands:** Corfú, unterhalb Strinilas, *Düll s.n.* (Hb. Düll). **Peloponnese:** Ilia, SE of Vasilakio, Alfios Valley, *Blockeel* (Hb. Blockeel 17/233, United Kingdom). **Thessalia:** Mt. Pelion, *Rechinger 23760* (S). **Thrace:** bei der Lande nördlich von Alexandroupolis, *Rechinger 23744* (S). HUNGARY. **Borsod-Abaúj-Zemplén:** Hegyalja hills, Finámcdomb hill in Tokaj, *Pócs & van Zanten 96107/B* (MO). **Győr-Moson-Sopron:** Sokoró hills, valley Likas Horong, SW from Ravazd, *Pócs &*

van Zanten 9691/DA (MO). **Komárom-Esztergom:** Gerecse Mts., forest W of Tardosbánya, *Pócs & van Zanten 96120/CA* (MO). ITALY. **Puglia:** Puglia, Gargano, *Sabovljevic s.n.* (CAME). **Calabria:** Crotone, Verzino, Grave di Grubbo, *Puntillo s.n.* (CLU B1293). **Campania:** Caserta, *Terracciano s.n.* (RO). **Sardegna:** S. Elia, Cagliari, *Cogoni s.n.* (Hb. Cogoni, Italy). **Emilia-Romagna:** Colli Reggiani ad Dinazzano, *Fiori s.n.* (RO). **Friuli-Venezia Giulia:** Triest, *Kerner s.n.* (GJO). **Liguria:** San Remo, *Norris s.n.* (JE). **Lombardia:** Como, *Möller s.n.* (S). **Piemonte:** prope Torino, *De Notaris s.n.* (RO). **Sicilia:** Messina, *Zodda s.n.* (S). **Toscana:** Bosco di Larioni, ad orient. Florentiae, *Levier s.n.* (WU). **Trentino-Alto Adige:** Bozen, *Suse s.n.* (S). PORTUGAL. **Algarve:** Fontes Grandes Altas, *Casas et al. s.n.* (LISU 154945). **Beira Litoral:** entre Albergaria dos Doze e Cartania, *Jiménez s.n.* (MUB 12524). **Estremadura:** Serra da Arrábida, Mata do Solitario, *Sérgio s.n.* (COI 485). **Ribatejo:** a 6 km de Permeo para Torres Novas, *Melo s.n.* (LISU). ROMANIA. Moldova, Barnova, *Constantineau s.n.* (WU). RUSSIA. **Adygeya:** Kamennomostskij, Rufabgo Creek valley, *Ignatov s.n.* (SINU). **Karachaevo-Cherkessia:** Teberda Nature Reserve, Oriuchat Gorge, *Onipchenko 154/94* (SINU). **Krasnodar Kraj:** Black Sea coast area near Sochi, khosta brach of Caucasian State Reserve, *Ignatov & Ignatova s.n.* (SINU). SERBIA AND MONTENEGRO. **Montenegro:** near Becici SE of Budva, *Touw 7846* (L). **Serbia:** Beska, Srem, *Sabovljevic s.n.* (Hb. Sabovljevic 1014). SLOVAKIA. Velke Zaluzie, near Nitra, *Peciar et al. s.n.* (E). SLOVENIA. Wurmberg bei Pettau, *Glowacki s.n.* (GJO, GZU); Fraslan bei Cilli, *Glowacki s.n.* (WU). SPAIN. **Álava:** Amárita, *Heras 995/81* (VIT 1330). **Almería:** Venta de los Yesos, *Guerra s.n.* (MUB 2301). **Asturias:** Caso, Coballes, *Fernández-Ordoñez s.n.* (FCO 291). **Barcelona:** Seva, *Casas s.n.* (BCB 14670). **Cantabria:** Puente Viesgo, *Aedo s.n.* (BCB 30562). **Castellón:** Eslida, *Casañ s.n.* (VAL 3074). **Gerona:** La Molina, *Casas s.n.* (BCB 40007). **Granada:** Sierra Nevada, Barranco de San Juan, *Gil & Martínez s.n.* (GDA 13218). **Huesca:** Valle de Bujaruelo, *Cano et al. s.n.* (MUB 8471). **La Coruña:** Corrubedo, *Reinoso s.n.* (SANT 2757). **Lérida:** Pallars Sobirá, Escart, *Casas s.n.* (BCB 32841). **Málaga:** Marbella by Ronda, *Størmer s.n.* (O). **Murcia:** La Selva, *Ros s.n.* (MUB 368). **Navarra:** Ozcoidi, *Urdino s.n.* (PAMP 2579). **Teruel:** Villarluengo, Muela Mujer, *Puche s.n.* (VAL 2032). **Valencia:** Quesa, carretera a Bicorp, *Puche s.n.* (VAL 5072). **Valladolid:** pr. Portillo, *Cano s.n.* (MUB 15045). **Vizcaya:** Orozco, *Heras 194/86* (VIT 7925). **Zaragoza:** Mequinenza, *Casas s.n.* (BCB 408). SWEDEN. **Skaraborg:** in monte Kinnekulles, Westrogothia, *Zetterstedt s.n.* (RO). **Stockholm:** Stockholm, *Lindberg s.n.* (WU). **Uppsala:** Upssala, *Zetterstedt s.n.* (GJO). SWITZERLAND. **Bern:** Kandersteg, *Wahnfchaff s.n.* (GJO). UNITED KINGDOM. **England:** Leicester, *Jackson s.n.* (GB).

3. Didymodon ferrugineus (Schimp. ex Besch.) M. O. Hill, J. Bryol. 11: 599. 1981 [1982]. *Barbula ferruginea* Schimp. ex Besch., Mém. Soc. Sci. Nat. Cherbourg 16: 181. 1872. *Triquetrella ferruginea* (Schimp. ex Besch.) Thér., Smithsonian Misc. Collect. 85(4): 9. 1931. TYPE: "Mexico," *F. Müller s.n.* (lectotype, designated by Zander (1981: 402), PC!; isotype, BM!). Figure 3A–E.

Barbula rigidicaulis Müll. Hal., Nuovo Giorn. Bot. Ital. 4: 255. 1897. TYPE: "China interior, provincia Schensi sept., Pou-o-li," 7 Mar. 1895, *J. Giraldi s.n.* (lectotype, designated here, FI!).

Barbula falcifolia Müll. Hal., Nuovo Giorn. Bot. Ital. 4: 257. 1897. TYPE: "China interior, provincia Schensi sept., She-kin-tsuen (Hu-schien)," 28 Dec. 1895, *J. Giraldi s.n.* (lectotype, designated here, H-BR 236005!).

Barbula serpenticaulis Müll. Hal., Nuovo Giorn. Bot. Ital. 5: 183. 1898. TYPE: "China interior, provincia Schen-si sept., in monte Tui-Kio-san, inter Mnia," 19 Oct. 1896, *J. Giraldi s.n.* (lectotype, designated here, FI!).

Plants (0.5–)0.8–3(–5) cm high, growing in loose turfs, brown-green or reddish brown; *stems* erect or ± decumbent, simple or branched, central strand weakly differentiated; *rhizoidal tubers* absent. *Leaves* appressed or incurved, slightly spirally twisted when dry, mainly the upper leaves, sometimes three-ranked, strongly recurved to squarrose, not undulate when moist, ovate-lanceolate, gradually narrowed to the apex, keeled, long-decurrent at base, (0.5–)0.7–2.0(–2.4) × (0.23–)0.35–0.85 mm; lamina unistratose, dark red with KOH stain; apex acute; margins entire, sometimes papillose-crenulate, recurved in the lower part, plane in the upper part of the leaf; *costa* (25–)30–60(–75) μm wide at leaf base, ending below the apex or percurrent, ventral cells of the costa in upper leaf elongated, smooth or papillose, dorsal cells of the costa in upper leaf quadrate, papillose, in transverse section at leaf base semicircular, with 2 to 3 guide cells in 1 layer, without ventral stereids, 0 to 1 layer of dorsal stereids, with or without ventral epidermis, smooth, dorsal epidermis differentiated, papillose or smooth; *upper and middle laminal cells* rounded to irregularly hexagonal, generally oblate, sometimes sinuous, 5–13 × (4–)5–12.5 μm, with (1 to)2 to 4 simple or bifurcate, tall papillae per cell, thick-walled, collenchymatous; *basal cells* shortly rectangular to rectangular, not sinuous, (8–)10–50 × 4–10(–12.5) μm, papillose or smooth, thick-walled, not pitted. *Gemmae* in the leaf axils absent. *Dioicous. Sporophyte* not seen.

Habitat and distribution. Calcareous or acidic (granite, schist) rocks with accumulated soil or fissures, artificial walls, soils or taluses generally in shaded places; 20–2000 m; North America (Zander, 2002), Central America (Allen, 2002), temperate and tropical Asia, Europe.

Discussion. *Barbula rigidicaulis* was described by Müller (1896) from material collected by Giraldi: "China interior, prov. Schen-si septentr., in loco dicto Pouo-li, Martio 1895." As previously mentioned, Müller's herbarium was lost in World

War II. In Biondi's herbarium at FI, we detected a syntype that matches the locality and date indicated in the protologue. We select this material as lectotype.

In Levier's herbarium at FI we found some of Müller's syntypes of *Barbula falcifolia* collected by Giraldi. We only found three specimens collected by Giraldi, none of which matched the only specimen provided in the protologue. Following Stafleu and Cowan (1981), we checked other herbaria where Müller's material could have been preserved and found a syntype in H-BR from the Bryotheca of Levier, which is in accord with the protologue. This was selected as lectotype.

The protologue of *Barbula serpenticaulis* has the information "China interior, prov. Schen-si sept., in monte Tui-kio-san, Oct. 1896." In Biondi's herbarium at FI we found two syntypes that match the locality and date indicated in the protologue. Both syntypes were collected by Giraldi but on different dates (19 Oct. 1896 and 21 Oct. 1896). We here choose the specimen dated 19 Oct. 1896 because it is better preserved.

Didymodon ferrugineus is characterized by its sometimes 3-ranked leaves that are strongly recurved to squarrose when moist, transverse section of the costa with 2 to 3 guide cells in 1 layer, without ventral stereids, and the strong papillosity of the lamina cells with simple or bifurcate papillae. *Didymodon ferrugineus* may be confused with *D. fallax*, but this latter species is differentiated by having erect-patent to spreading leaves that are rarely slightly recurved, but never squarrose. Furthermore, *D. fallax* generally has 1 to 2 layers of ventral stereids and (2 to)3 to 5(to 6) guide cells in 1 layer, while *D. ferrugineus* lacks ventral stereids and has 2 to 3 guide cells in 1 layer.

None of the specimens studied was fruiting, although according to Zander (1998), in reference to American specimens, the sporophyte is rare and similar to, but often smaller than, that of *D. fallax*.

Selected specimens examined. PAPUA NEW GUINEA. **Morove:** Mt. Sarawaket southern range 4 km SE of Lake Gwam, headwaters of Busu R., *Koponen 32170* (E). TURKEY. **Trabzon:** Pontic Mts., Black Sea coast, at Sumela monastery by Trabzon, *Papp s.n.* (BP 168092). AUSTRIA. **Salzburg:** Plainerau bei Salzburg, *Zwanziger s.n.* (WU). **Steiermark:** prope Hieflau, *Breidler s.n.* (WU). **Tirol:** Kufstein, *Wahnfchaff s.n.* (HBG). **Vorarlberg:** Kammelbach bei Bregenz, *Blumrich s.n.* (WU). BELGIUM. Vieilles ruines, Liresse, *Belogne s.n.* (HBG). CROATIA. Velebit-Gaviah, Tuljana, Juana bei Medak, *Degen s.n.* (W 22746). CZECH REPUBLIC. Koda, ca. 5 km SE of Beroun, *Townsend s.n.* (E); Tetin, *Bauer s.n.* (GJO). FRANCE. **Alpes-Maritimes:** Tenda, bei Nizza, *Hautl s.n.* (S). **Doubs:** Source de la Loue near Ouhans, *Touw 13234* (L). **Haute-Garonne:** Pyrénées Centrales, vallée d'Hospice, *Zetterstedt s.n.* (S). **Haute-Savoie:** Saint-Jean-d'Aulps, *Bizot s.n.* (S). **Hautes-Pyrénées:** Pyrénées, Béart, *Spruce s.n.* (S). **Isère:** Villard-de-Lans, *Ravaud s.n.* (LISU 4331). **Savoie:** Mont-Denis, Cret Verdan, *Een F442* (S). GERMANY. **Baden-Württemberg:** Lichtenstein, *Ros & Werner s.n.* (MUB 17221). **Bayern:** Fränkische Schweiz, Pottenstein, bei der Schüttersmühle, *Elmendorff s.n.* (GJO). GEORGIA. Imeretia, Utseri, in ripa fl. Rion, *Brotherus & Brotherus s.n.* (LE). ITALY. **Friuli-Venezia Giulia:** Peitlstein prope Ampezzo, *Molendo s.n.* (HBG, L, S). **Toscana:** Appenino pistoiese, *Cortini-Pedrotti s.n.* (CAME). **Trentino-Alto Adige:** Brenner-Pass, *Een s.n.* (S). **Veneto:** Vittoria am Monte Canzeglio, *Fleischer s.n.* (BM, WU). RUSSIA. **North Ossetia:** Ossetia, Balta ad fl. Terek, *Brotherus & Brotherus s.n.* (LE). SLOVENIA. Flitsch, *Breidler s.n.* (WU); Fraslan bei Cilli, *Glowacki s.n.* (WU). SPAIN. **Álava:** Zeanuri, Almadin, *Infante s.n.* (VIT). **Barcelona:** Sierra de Montserrat, *Casas s.n.* (BCB 434). **Cantabria:** Picos de Europa, Mts. Refugio Aliva, *Henderson 2017a* (E). **Gerona:** entre Beget y Rocabruna, *Casas s.n.* (BCB 19941). **Guipúzcoa:** Berástegui, Valle de Leizarán, *Heras 685/92* (VIT 15337). **Huesca:** Escalona, Añisclo, ermita de San Úrbez, *Cano et al. s.n.* (MUB 8491). **León:** Cabrillanes, próximo Cacabillo, *Muñoz s.n.* (MA 19277). **Lérida:** Lladorre, *Casas s.n.* (PAMP 568). **Lugo:** Ribadeo, Miguxín, *Muñoz s.n.* (MA 17515). **Navarra:** Elzaburu, *Lurso s.n.* (PAMP 5481). **Teruel:** Alcalá de la Selva, *Casas s.n.* (BCB 432). SWITZERLAND. **Bern:** Interlaken nach Därlingen, *Culmann s.n.* (GJO, WU). **Tessin:** Lugano, *Salvatore s.n.* (WU). **Zürich:** Zürich, *Forsder s.n.* (HBG). UNITED KINGDOM. **England:** Cornwall, Penzance, *Curnow s.n.* (GJO). **Northern Ireland:** Marble Arch., *Sérgio & Geissler s.n.* (LISU).

4. **Didymodon giganteus** (Funck) Jur., Laubm.-Fl. Oesterr.-Ung.: 102. 1882. *Barbula gigantea* Funck, Flora 15: 483. 1832. *Grimmia gigantea* (Funck) Schimp., Syn. Musc. Eur.: 695. 1860. *Tortula gigantea* (Funck) Lindb., Öfvers. Förh. Kongl. Svenska Vetensk.-Akad. 21: 250. 1864. *Geheebia gigantea* (Funck) Boulay, Musc. France: 395. 1884. TYPE: [Austria.] "Kärnten, Gössnitzerfall bei Heiligenblut," *J. F. Laurer s.n.* (lectotype, designated here, HBG!). Figure 4A–F.

Didymodon levieri Broth., Nuovo Giorn. Bot. Ital. 13: 256. 1906. TYPE: "China interior, provincia Schen-si septentr. in monte Ki-tou-san," Sep. 1899, *J. Giraldi s.n.* (lectotype, designated here, H-BR 1291005!).

Didymodon subrufus Broth., Symb. Sin. 4: 38. 1929. TYPE: [China.] "Provincia Setschwan austro-occid, in montis Liuku-liangdse, 27°48′, inter oppidum Yenyüen et castellum Kwapi, 3700–4200 m," 18 May 1914, *H. F. v. Handel-Mazzetti 2353* (holotype, H-BR 1291039!).

Plants (3–)7–23 cm high, growing in ± dense turfs, reddish brown or brown-green; *stems* erect or decumbent, irregularly branched, central strand weakly differentiated; *rhizoidal tubers* absent. *Leaves* appressed in the lower part of stem, spirally twisted in the upper part when dry, erect-patent to

spreading, undulate when moist, ovate-lanceolate, gradually narrowed to the apex, sometimes with small plicae at the base, keeled, long-decurrent at base, (2–)2.5–4–5 × 0.7–1.1 mm; lamina unistratose, red with KOH stain; apex acute; margins entire, recurved in lower part, plane in upper part of the leaf; *costa* 42–85 μm wide at leaf base, ending below the apex or percurrent, ventral cells of the costa in upper leaf elongated, smooth or papillose, dorsal cells of the costa in upper leaf rectangular, papillose, in transverse section at leaf base elliptic to semicircular, with 4 to 6 guide cells in 1 layer, 1 to 2 layers of ventral stereids, sometimes 1 layer of substereids, 1 to 2 layers of dorsal stereids, without ventral epidermis, without dorsal epidermis or weakly differentiated, smooth; *upper and middle laminal cells* oblate, sometimes rounded or rhomboidal, very irregular, strongly sinuous, (3–)4–17.5(–20) × 7.5–20 μm, with 1 to 3 simple or, more rarely, bifurcate, papillae per cell, sometimes apparently absent, thick-walled, strongly collenchymatous; *basal cells* rectangular, becoming shorter toward margins, sinuous, (15–)17.5–55 × 2–8 μm, smooth or papillose, thick-walled, pitted. *Gemmae* in the leaf axils absent. *Dioicous*. *Sporophyte* unknown.

Habitat and distribution. Wet calcareous rocks in waterfalls; 500–2300 m; North America (Zander, 2002), temperate and tropical Asia (Li et al., 2001), Europe.

Discussion. Funck (1832) described *Barbula gigantea* on the basis of two specimens collected by him and Laurer from two different localities ". . . nach Golling. . . ; . . . beim Gösnitzer Wasserfall. . . ." We have examined Funck's herbarium deposited at M but no specimen could be considered to represent a syntype. A search in other herbaria where Funck specimens are kept (BM, BUC, GOET, HAL, JE, TUB) was unsuccessful. Accidentally, we found a specimen collected by Laurer deposited in HBG, whose label shows the second locality mentioned in the protologue. Therefore, we select this material as lectotype.

The protologue of *Didymodon levieri* includes "In monte Ki-tou-san, parcissime; sett. 99." In Brotherus's herbarium at H we detected a syntype collected by Giraldi that matches the locality and date indicated in the protologue. We therefore choose this specimen as lectotype.

Since its description by Funck (1832), *Didymodon giganteus* has been included in several genera (*Tortula*, *Grimmia*, *Barbula*), and a monospecific genus (*Geheebia* Schimp.) has even been described for this taxon. Some authors (Corley et al., 1981; Düll, 1992; Frey et al., 1995; Cortini-Pedrotii, 2001) include this species in the genus *Geheebia*, but others (Saito, 1975; Zander, 1978; Kučera, 2000) consider it within the genus *Didymodon*. A careful study suggests that it does belong to *Didymodon* since it possesses all the morphological characteristics that define this genus. More specifically, *D. giganteus* belongs to section *Fallaces* since it presents the following fundamental characteristics: keeled leaves, decurrent margins, lamina unistratose, elongated cells on the ventral side of the costa, and red-staining lamina with KOH. Molecular data obtained from cp *rps*4 sequence (Werner et al., 2004a) confirm the close relation between this species and others of the genus *Didymodon* suggested by our morphological study. It should not be considered as a separate genus.

This species is recognizable by its relatively enormous size, as it can reach as much as 23 cm in length, and by its ovate-lanceolate, keeled leaves that have undulate margins in the upper half of the leaf, very sinuous laminal cells, and porous basal cells.

A species with which *Didymodon giganteus* may be confused is *D. maximus*, since both share the same leaf shape, papillosity of the lamina, costa thickness, and the red color of the lamina with KOH. However, the wet leaves of *D. giganteus* are erect-patent to spreading, undulate, and (2–)2.5–4.5 mm long. The wet leaves of *D. maximus*, on the other hand, are strongly recurved or squarrose, not undulate, and are smaller in size, (1.2–)1.6–2.8 mm long.

Another close taxon is *Didymodon erosodenticulatus* (Müll. Hal.) K. Saito, a species known only from eastern Asia (China, Japan, Himalayas), where it shares a similar habitat as *D. giganteus*. However, *D. erosodenticulatus* can be differentiated from *D. giganteus* by its toothed, non-undulate upper leaf margin.

Selected specimens examined. AUSTRIA. **Kärnten:** Gössnitzfall näch Heiligenblut, *Handel-Mazzetti s.n.* (GJO, WU). **Niederösterreich:** Silberquelle am Schneeberg, *Handel-Mazzetti s.n.* (WU). **Oberösterreich:** Dachsteingebiet, oberhalb Hallstatt, *Fleischer s.n.* (BM, WU). **Salzburg:** Radstadt Tauern, *Breidler s.n.* (WU). **Steiermark:** inter cataractam "Todtes Weib" at vicum Frein, *Kerner s.n.* (WU). **Tirol:** Prosegg-Klamm, bei Windisch-Matrei, *Baumgartner s.n.* (HBG, WU). FRANCE. **Haute-Garonne:** Val d'Esquierry, *Juin s.n.* (BM, S). **Haute-Savoie:** Samoëns, *Sarrasat s.n.* (GB). **Hautes-Pyrénées:** Cascade du Gros, *Spruce s.n.* (S). GERMANY. **Bayern:** Allgäu, an der strasse von Hindelang nach Hinterstein, *Holler s.n.* (WU). ITALY. **Lombardia:** Como, stravalle bei Torno, *Artaria s.n.* (BM, GZU, M, WU). **Piemonte:** Novara, Bosco di Roncio bei Campello Monti, *Bauer s.n.* (GZU, WU). **Veneto:** "Serai," prope Sottoguda ditionis venetae, *Mo-*

lendo s.n. (M, W 359094). SLOVENIA. Kranjska gora Krain, *sine collector* (GJO). SLOVAKIA. Bielské Tatry, in monte Zdiarská Vidla, *Smarda s.n.* (L); Magas Tátra, montis "Stierberg," *Györffy s.n.* (GJO, HBG, WU). SWITZERLAND. **Bern:** Faulhorn, *Grebe s.n.* (GJO). **Glarus:** Glarus, *Culmann s.n.* (WU). **Graubünden:** Vall Roseg, bei Pontresina, *Graef s.n.* (HBG). **Uri:** Klausenpass, *Sérgio s.n.* (LISU). **Valais:** Cascade de Pissevache, *Favrat s.n.* (WU).

5. Didymodon maschalogena (Renauld & Cardot) Broth., Nat. Pflanzenfam. I(3): 1192. 1909. *Barbula maschalogena* Renauld & Cardot, Bull. Soc. Roy. Bot. Belgique 41(1): 53. 1905. TYPE: [India.] "Sikkim, Darjeeling," 1901, *G. A. Miller s.n.* (lectotype, designated by Frahm et al. (1996: 137), PC!). Figure 1D–H.

Barbula catenulata Dixon, Anniv. Vol. Bot. Gard. Calcutta: 181. 1942. TYPE: [India.] "Kashmir, Dalhousie," Oct. 1917, *Kinnear 510b* (holotype, BM!).

Didymodon michiganensis (Steere) K. Saito, J. Hattori Bot. Lab. 39: 517. 1975. *Barbula michiganensis* Steere, Moss Fl. N. Amer. 1: 180. 1938. TYPE: [U.S.A.] "Lake Superior at Pictured Rocks, Alger Co., Michigan," 20 Aug. 1935, *G. E. Nichols & W. C. Steere s.n.* (holotype, MICH not seen; isotype, DUKE!).

Plants to 1 cm high, growing in loose turfs, yellow-green; *stems* erect, simple, central strand differentiated; *rhizoidal tubers* absent. *Leaves* catenulate, incurved when dry, erect-patent to spreading, not undulate when moist, ovate to ovate-lanceolate, abruptly narrowed to the apex, keeled in the upper part, decurrent at base, 0.94–1.27 × 0.47–0.65 mm; lamina unistratose, red or yellowish with KOH stain; apex acuminate; margins entire, recurved from base to 2/3 of the leaf; *costa* 47.5–75 μm wide at leaf base, ending below the apex or percurrent, ventral cells of the costa in upper leaf elongated, smooth or papillose, dorsal cells of the costa in upper leaf shortly rectangular to quadrate, smooth or papillose, in transverse section at leaf base semicircular, with 2 to 4(to 5) guide cells in 1 layer, 0 to 1 layer of ventral stereids, 1 to 2 layers of dorsal stereids, ventral epidermis differentiated, smooth or papillose, dorsal epidermis differentiated, smooth or papillose; *upper and middle laminal cells* rounded, ovoid or oblong, not sinuous, (3–)4–10(–12.5) × 5–8(–10) μm, arranged in longitudinal rows, with one low, simple papilla or, more rarely, smooth, thick-walled, collenchymatous; *basal cells* rectangular or shortly rectangular, not sinuous, (15–)17.5–37.5(–50) × (5–)7.5–12.5(–15) μm, forming a ± differentiated area, smooth, thick-walled, not pitted. *Gemmae* multicellular, 2- to 8-celled, borne in the axils of the leaves, abundant, generally spherical, sometimes elliptical, 20–35(–45) μm diam., brown, smooth. *Sexual condition* unknown. *Sporophyte* unknown.

Habitat and distribution. On soil; Africa (O'Shea, 2003), North America, temperate and tropical Asia.

Discussion. This species is known from different areas of the world, although it has been reported from a very few scattered localities (Jiménez et al., 2004). It is difficult to confuse with other species of section *Fallaces* since it is the only taxon that has spherical or elliptical axillary gemmae. Another important characteristic of the species is the catenulate position of the leaves when dry, although its most obvious feature is the disposition of the upper and median cells along the lamina in longitudinal rows.

Representative specimen examined. IRAN. Mounts Elburz, *sine collector* (IRAN 4308).

6. Didymodon maximus (Syed & Crundw.) M. O. Hill, J. Bryol. 11: 599. 1981 [1982]. *Barbula maxima* Syed & Crundw., J. Bryol. 7: 527. 1973 [1974]. *Barbula reflexa* var. *robusta* Braithw., Brit. Moss Fl. 1: 266. 1887. TYPE: [Ireland.] "Dripping rocks, Ben Bulben, Sligo," 1871, *D. Moore s.n.* (lectotype, designated here, BM!). Figure 3F–H.

Plants (2–)3–10 cm high, growing in loose turfs, brown-green or reddish brown; *stems* erect, branched, without central strand or weakly differentiated; *rhizoidal tubers* absent. *Leaves* appressed to slightly spirally twisted when dry, strongly recurved to squarrose, not undulate when moist, ovate-lanceolate, gradually narrowed to the apex, keeled, long-decurrent at base, (1.5–)2–2.8 × 0.5–1.1 mm; lamina unistratose, dark red with KOH stain; apex acute, rarely obtuse; margins entire or papillose-crenulate, almost plane to recurved in the lower middle part, more rarely in the proximal 3/4 of the leaf; *costa* 40–90(–125) μm wide at leaf base, ending below the apex or percurrent, ventral cells of the costa in upper leaf elongated, smooth or papillose, dorsal cells of the costa in upper leaf rectangular or quadrate, smooth or papillose, in transverse section at leaf base elliptic, with (3 to)4 to 8(to 9) guide cells in 1 layer, very rarely in 2 layers, 1 to 3 layers of ventral stereids, 1 to 3(to 4) layers of dorsal stereids, without ventral epidermis or weakly differentiated, smooth or papillose, dorsal epidermis generally differentiated, smooth or papillose; *upper and middle laminal cells* rounded, ovoid or shortly rectangular, oblate or not, sinuous, (3–)5–17.5 × 5–15 μm, almost smooth or with 1

to 3 simple or bifurcate, tall papillae per cell, thick-walled, collenchymatous; basal cells rectangular, sometimes sinuous, 12.5–50 × 3–10 μm, papillose or smooth, thick-walled, not pitted. *Gemmae* in the leaf axils absent. *Dioicous*. *Seta* erect, 1.2 cm long, orange-reddish, spirally twisted to left throughout; *sporophyte* otherwise unknown.

Habitat and distribution. Wet ledges or damp soil at the foot of limestone rocks; North America (Zander, 2002), Europe.

Discussion. Syed and Crundwell (1973) established *Barbula maxima* as a new name on the basis of the type specimen of *Barbula reflexa* var. *robusta*. The protologue of this latter taxon includes: "Limestone rocks at Ben Bulben, Sligo (Moore)." We have studied the collections of *Barbula reflexa* var. *robusta* in Braithwaite's herbarium in BM, and we found a syntype collected by Moore dated in 1871, which is in complete accordance with the protologue. We therefore select this material as lectotype.

Didymodon maximus is a rare taxon known only from two sites in the northwest of Ireland, one in Alaska, and another in Canada (Northwest Territories) (Zander, 2002). This species demonstrates a distinctive disjunct pattern between western North America and the west of Europe.

Didymodon maximus is close to *D. ferrugineus*, from which it differs almost exclusively in the length of its leaves: (0.5–)0.7–2 mm long in *D. ferrugineus* and (1.5–)2–2.8 mm long in *D. maximus*, and in costa structure: (3 to)4 to 8(to 9) guide cells in 1 layer or more rarely in 2, 1 to 3 layers of ventral stereids, 1 to 3(to 4) layers of dorsal stereids in *D. maximus* compared with the 2 to 3 guide cells arranged in 1 layer, without ventral stereids and 0 to 1 layer of dorsal stereids in *D. ferrugineus*. Furthermore, the plants of *D. maximus*, (0.5–)0.8–4(–5) cm in height, are usually much bigger than plants of *D. ferrugineus*. Syed and Crundwell (1973) stated that *D. maximus* has a clearly developed central strand as opposed to the only slightly differentiated central strand of *D. ferrugineus*, a characteristic they used to differentiate between both taxa. However, all the specimens of *D. maximus* studied by us showed no or, at most, a very slightly differentiated central strand, so that the species could not be separated by reference to this feature.

It was not possible to describe the capsule since the only fertile specimen known (*Long 14626*) has immature or undeveloped capsules.

Didymodon maximus was recently cited from the French Pyrenees (Thouvenot, 2002), but this was based on an erroneous interpretation of the original citation.

Selected specimens examined. IRELAND. **Leitrim:** Glenade, *Duncan s.n.* (E). **Sligo:** Gleniff above Clogh, below cliffs, *Long 14626* (E).

7. Didymodon spadiceus (Mitt.) Limpr., Laubm. Deutschl. 1: 556. 1888. *Tortula spadicea* Mitt., J. Bot. 5: 326. 1867. *Trichostomum spadiceum* (Mitt.) J. E. Zetterst., Kongl. Svenska Vetenskapsakad. Handl. 13(14): 14. 1876. *Barbula spadicea* (Mitt.) Braithw., Brit. Moss Fl. 1: 267. 1887. *Didymodon rigidulus* subsp. *spadiceus* (Mitt.) Adlerz, Bladmossfl. Sver. Lågland 171. 1907. *Barbula rigidula* subsp. *spadicea* (Mitt.) J. J. Amann, Fl. Mouss. Suisse 2: 103. 1918. *Barbula fallax* subsp. *spadicea* (Mitt.) Hillier, Ann. Sci. Univ. Besançon, Sér. 2, Bot.: 48. 1954. TYPE: [United Kingdom.] "Yorkshire, near Bolton Abbey," Oct. 1837, *Wilson s.n.* (lectotype, designated here, NY!). Figure 5E–I.

Barbula insidiosa Jur. & Milde, Hedwigia 8: 97. 1869. TYPE: [Austria.] "Hagenbach bei St. Andrä in Niederösterreich," 25 Apr. 1869, *J. Juratzka s.n.*, Bryoth. Eur. nº 1067 (lectotype, designated here, RO!; isotypes, C!, MO!, WU!).

Didymodon barbuloides Lib. ex Marchal., Bull. Soc. Roy. Bot. Belgique 11: 8. 1872. Syn. nov. TYPE: Locality not indicated, [sine collector] (lectotype, designated here, BR74416!).

Didymodon zetterstedtii Schimp., Syn. Musc. Eur. (ed. 2): 167. 1876. TYPE: [Sweden.] "Kinnekulle," 18 Aug. 1853, *J. E. Zetterstedt 17* (holotype, BM!).

Limneria viridula Stirt., Trans. & Proc. Bot. Soc. Edinburgh 26: 428. 1915. TYPE: [United Kingdom.] "Scotland, near Plockton," Aug. 1914, [sine collector] (lectotype, designated here, Hb. Stirton in BM!).

Plants (0.4–)0.7–4 cm high, growing in ± dense turfs, brown-green; *stems* erect, simple or branched, central strand differentiated; *rhizoidal tubers* absent. *Leaves* twisted, slightly appressed to incurved when dry, erect-patent to spreading, not undulate when moist, sometimes slightly flexuous, long ovate-lanceolate, gradually narrowed to the apex, not keeled, slightly decurrent at base, (1–)1.5–4(–4.5) × (0.3–)0.45–1(1.2) mm; lamina unistratose, red-orange with KOH stain; apex obtuse, sometimes acute; margins entire or papillose-crenulate, recurved in the lower middle of the leaf, very rarely to 2/3 of the leaf; *costa* 60–180(–220) μm wide at leaf base, ending below the apex or percurrent, ventral cells of the costa in upper leaf elongated, smooth, dorsal cells of the costa in upper leaf shortly quadrate, papillose, in transverse section at leaf base semicircular, with (4 to)5 to 9(to 10) guide

cells in 1 layer, very rarely in two layers, (1 to)2 to 3(to 4) layers of ventral stereids, 2 to 3(to 4) layers of dorsal stereids, without ventral epidermis or weakly differentiated, papillose or smooth, dorsal epidermis differentiated, papillose; *upper and middle laminal cells* ovoid, irregularly rounded or subquadrate, sometimes very slightly sinuous in the middle of the leaf, (4–)5–15 × (4–)5–12.5(–15) μm, with 1 to 3 simple or bifurcate papillae per cell, thick-walled, collenchymatous; *basal cells* rectangular, sometimes slightly sinuous, 10–50 (–65) × 5–12.5 μm, smooth or papillose, generally thick-walled, not pitted. *Gemmae* in the leaf axils absent. *Dioicous. Seta* erect, 0.7–2.5 cm long, reddish brown, spirally twisted to left throughout; *capsule* erect or slightly inclined, cylindrical to oblong, 1.3–4.3 × 0.3–0.7 mm, brown; *peristome* of 16 teeth cleft to near base, filiform, smooth or papillose, straight, (100)135–450(650) μm long, brown-reddish; *operculum* long-rostrate, 0.8–1.6 mm long; *calyptra* cucullate, 1.5–3.1 mm. *Spores* spherical, 8–15 μm diam., weakly papillose, brown-green.

Habitat and distribution. On calcareous rocks, more rarely on acidic rocks, on wet taluses at edges of streams and rivers, also on artificial walls; 150–1680 m; temperate Asia, Europe.

Discussion. Mitten (1867) cited several specimens in the protologue of *Tortula spadicea*: "Scotland, Drummond. Yorkshire, near Bolton Abbey, Mr. Wilson. Ireland, Miss Hutchins." In Mitten's herbarium at NY we found two syntypes. On the label of one of the specimens was written "Ireland" and in the other "Yorkshire, near Bolton Abbey." We select this latter specimen as lectotype since it is better preserved.

In the protologue of *Barbula insidiosa*, Juratzka (1869) cited material from different localities: "Grunauer bei Hirschberg in Schlesien (Ilgner); Wien (Juratzka); Meran (Milde); Westphalen: Sauerland (H. Müller)." The same author also mentioned that some material of this taxon was going to be issued in *Rabenhorst Bryotheca Europaea* (Nr. 1067). We did not find any syntype in W, where the Juratzka specimens are deposited. However, we have located several specimens of Rabenhorst's exsiccatae in different herbaria (C, MO, RO, WU). We select the specimen deposited in WU because it is better conserved than the other specimens.

Didymodon barbuloides was described by Marchal (1872) on the basis of several specimens collected by Libert. The protologue of this taxon does not include any reference to the locality or localities of the collection: "In rupibus arenariis umbrosis. Autumno." We found a syntype at BR, where the original herbaria of Libert and Marchal are kept. This specimen is in accordance with the protologue so we select it as lectotype. After examining this material, we conclude that there are no significant morphological differences between this taxon and *D. spadiceus.*

The protologue of *Limneria viridula* includes "It grows in several places on the west coast of Scotland, but most luxuriantly near the base of the famous Duncraig." We have checked Stirton's herbarium in GLAM, but found no material suitable for a lectotype. According to Stafleu and Cowan (1986), some of Stirton's material can be found in BM. We located two possible specimens from the Stirton herbarium in BM whose label shows the same locality (Scotland, near Plockton). One of these specimens corresponds to *Didymodon insulanus* (De Not.) M. O. Hill, so we choose as lectotype the other material, which is in accordance with the protologue.

Didymodon spadiceus is characterized by its erect-patent to spreading leaves when moist, their long ovate-lanceolate shape and generally obtuse apex, margins recurved in the lower half of the leaf, occasionally to 2/3 of the leaf, and the transverse section of costa showing generally 1 layer of (4 to)5 to 9(to 10) guide cells. In addition, the sporophyte has short peristome teeth (100–)135–450(–650) μm that are long and straight.

Occasionally especially large specimens of *D. fallax* may be found in mountainous regions, with long, ovate-lanceolate leaves, stout costa more than 100 μm wide at base, and strongly papillose laminal cells with bifurcated papillae and slightly sinuous lumens [*Casas et al. s.n.* (BCB 32841)], which are difficult to distinguish from *D. spadiceus.* The sporophytes of these two species, however, are clearly different.

Selected specimens examined. IRAN. **Mazandaran:** in valle fluvii Talar inter Abbasabad et Cahi, *Rechinger 2268* (W); above Shahi, Caspian coast, *Agnew s.n.* (NMW). ANDORRA. La Massana Parish, Arinsal, *Townsend 98/118* (E). AUSTRIA. **Kärnten:** Feistritz-Thale, *Robic s.n.* (WU). **Niederösterreich:** Helenenthal bei Baden, *Handel-Mazzetti s.n.* (WU). **Steiermark:** Salzaufer beim Holzrechen, *Baumgartner s.n.* (WU). **Tirol:** Nord-Tirol, Sellrain, *Handel-Mazzetti s.n.* (WU). **Vorarlberg:** Feldkirch, *Handel-Mazzetti s.n.* (WU). BOSNIA HERZEGOVINA. Bistrica bei Foca, *Glowacki s.n.* (GJO); Lapesnica bei Sarajevo, *Glowacki s.n.* (GJO). BULGARIA. **Plovdiv:** Mt. Rhodope centralis, Er-Kjupria, *Petrov s.n.* (SOM). CROATIA. Istrien, Draga-Tal bei Vermo, *Glowacki s.n.* (GJO); Velebit-Gaviah, Tuljana bei Medak, *Baumgartner s.n.* (W 23154). CZECH REPUBLIC. Moldau bei Stechowitz, *Bauer s.n.* (HBG). FRANCE. **Doubs:** Cirque de Consolation N of Morteau, *Touw 13166* (L). **Haute-Savoie:** Fessy, *Puget s.n.* (S). **Hautes-Pyrénées:** Labassére, V. de Béart, G. de Valentin, *Spruce s.n.* (S). **Isère:** Le Bourg

d'Arud, cascade du ruisseau de la Pisse au Sud du village, *De Sloover s.n.* (MO). **Jura:** Source de l'Ain, *Cuynet s.n.* (BCB 1749). **Meuse:** Vallée de Froide, Fountaine, *Cardot s.n.* (MO). **Pyrénées Orientales:** Amélie-les-Bains, *Buterte s.n.* (S). **Pyrénées-Atlantiques:** Beost, *Spruce s.n.* (S). **Sarthe:** Le Mans francs à l' Epau, *Monguillon s.n.* (WU). **Tarn-et-Garonne:** Pyrénées Centrales, Cascade de Montauban, *Zetterstedt s.n.* (S). GEORGIA. **Abkhazia:** Tsebelda, *Kopakovskij s.n.* (LE); Angrestiae Pelznir, *Woronow s.n.* (LE). GERMANY. **Bayern:** prope Wildflecken, *Geheeb s.n.* (RO). **Brandenburg:** Potsdam, *Giordano s.n.* (RO). **Hesse:** prope Rengersfeld (mont. Rhon), *Geheeb s.n.* (RO). **Nordrhein-Westfalen:** bei Alme, *Grebe s.n.* (WU). **Sachsen:** Kirnitzschtal, *Riehmer s.n.* (GJO). **Sachsen-Anhalt:** Harz, Treseburg, *Loeske s.n.* (WU). **Thüringen:** Walpernhain prope Orterfeld, *Schliephacke s.n.* (RO). GREECE. **Macedonia:** Pierfa, Olympo, umgebung der Prinias-Wasserfälle, straßenende Lithodorion, *Düll s.n.* (Hb. Düll); 2 km SW Veria, *Wolff & Loosjes 4* (L). HUNGARY. **Borsod-Abaúj-Zemplén:** Borsod, prope Hamor, *Boros s.n.* (MO). **Budapest:** Budapest, Pest, *Boros s.n.* (MO). ITALY. **Friuli-Venezia Giulia:** strasse von Maggio gegen Venzone, *Breidler s.n.* (GJO). **Lazio:** Roma, Circo Romano, *Poli s.n.* (RO). **Lombardia:** Bellagio, *Giovani s.n.* (S). **Trentino-Alto Adige:** Monte Bondone, *Cortini-Pedrotii s.n.* (CAME). **Umbria:** Interamnae (RO). ROMANIA. **Harghita:** Transilvania, Ciuc, prope balneas Borsec, *Demeter s.n.* (MO). RUSSIA. **Adygeya:** Caucasian Reserve, Maikop, in Zhelobnaya River, *Vasilieva s.n.* (LE). SERBIA AND MONTENEGRO. **Montenegro:** Kom, *Glowacki s.n.* (GJO); Monastir Morački, *Glowacki s.n.* (GJO). SLOVENIA. Gebiet von Görz bei Flitsch, *Breidler s.n.* (GJO). SPAIN. **Álava:** Aspárrena, Andoin, La Tobería, *Heras 782/82* (VIT 2198). **Asturias:** Somiedo, carretera al Puerto, pr. Gúa, *Muñoz s.n.* (MA 16434). **Baleares:** Mallorca, cruce de carretera Sacalobra y carretera a Pollensa, *Cano et al. s.n.* (MUB 11938). **Cantabria:** Camaleño, próximo las Ilces, *Muñoz s.n.* (MA 19194). **Cuenca:** Hoz de Beteta, Río Guadiela, *Fuertes-Lasala & Silva s.n.* (MA 306). **Gerona:** El Coll, *Vives s.n.* (BCB 35617). **Guipúzcoa:** Aya, Barranco de Azolaras, *Heras 1450/95* (VIT 19655). **Huesca:** Valle de Pineta, Bielsa, *Casas s.n.* (BCB 49867). **León:** Villablino, *Allorge & Allorge s.n.* (B). **Navarra:** Arbayún, *de Miguel s.n.* (PAMP 2767). **Vizcaya:** Orozco, Urigoiti, torrentera de Aldabide, *Heras 421/90* (VIT 13663). SWEDEN. **Östergötland:** Väversunda, Anudden, W Mt. Omberg, *Hallingbäck 38779* (MUB 14118). UNITED KINGDOM. **England:** prope Burnley, *Nowell s.n.* (RO).

8. **Didymodon tomaculosus** (Blockeel) M. F. V. Corley, J. Bryol. 11: 649. 1981 [1982]. *Barbula tomaculosa* Blockeel, J. Bryol. 11: 583. 1981. TYPE: [United Kingdom.] "Midgley near Wakefield," 6 Jan. 1980, *T. L. Blockeel s.n.* (holotype, CGE!; isotype, Hb. T. L. Blockeel!). Figure 1A–C.

Plants 0.2–0.9 cm high, growing in very loose turfs, dark green or reddish brown; *stems* erect, simple, without central strand or weakly differentiated; *rhizoidal tubers* underground or on rhizoids on lower stem, multicellular, with one or several shining globules per cell, rounded to elongate, straight or variously curved, 30–145 × 22–45 μm, brown, smooth. *Leaves* sparse along the stem, incurved or spirally twisted, appressed to erect-patent when dry, patent to spreading, more rarely recurved, not undulate when moist, lanceolate to ovate-lanceolate, acuminate, generally keeled in the upper part, slightly decurrent at base, 0.7–2.1 × 0.25–0.58 mm; lamina unistratose, yellow to reddish orange with KOH stain; apex acute; margins entire, recurved from base to ¾ of the leaf; *costa* 30–87.5 μm wide at leaf base, shortly excurrent or percurrent, ventral cells of the costa in upper leaf quadrate or rectangular, smooth, dorsal cells of the costa in upper leaf quadrate or rectangular, smooth, sometimes with low papillae, in transverse section at leaf base semicircular or elliptic, with 2 to 4(to 5) guide cells in 1 layer, without ventral stereids, 1(to 2) layers of dorsal stereids, ventral epidermis differentiated, smooth, dorsal epidermis differentiated, smooth; *upper and middle laminal cells* quadrate to shortly rectangular, oblate or not, not sinuous, 5–17.5 × 5–12.5 μm, smooth or with low papillae, thin-walled or slightly thickened, collenchymatous; *basal cells* quadrate to rectangular, not sinuous, 10–37.5 × 5–10 μm, smooth, thin-walled, not pitted. *Gemmae* in the axils of the leaves absent. *Dioicous. Sporophyte* unknown.

Habitat and distribution. Arable fields; Europe.

Discussion. A rare taxon known from very few stations in the United Kingdom and only two localities in Ireland (Hill et al., 1992). The Irish collections consist of poor material detected under the microscope and appear to have come from a more friable soil than the English plants (Hill et al., 1992). This was considered an endemic to the British Isles until Koperski et al. (2000) cited it from one site in the south of Germany.

Didymodon tomaculosus is principally characterized by the presence of numerous rhizoidal tubers that are subterranean or on the rhizoids on lower stems. Stems have a weakly differentiated, sometimes absent, central strand and widely spaced leaves along the stem. The costa is shortly excurrent or percurrent, without ventral stereids, the lamina cells are generally smooth although they may show low papillae, which can only be observed in cross section.

Didymodon tomaculosus forms small turfs loosely interwoven with other mosses. This habit and its small size, together with its morphological similarity to *D. fallax*, mean that the taxon may easily be confused with *D. fallax* or even completely overlooked. *Didymodon tomaculosus* differs from *D. fallax* mainly by having square or shortly rectangular

cells on the ventral side of the costa in the upper half of the leaf (vs. elongated in *D. fallax*) and by the presence of rhizoidal tubers (vs. absent).

Selected specimens examined. UNITED KINGDOM. **England:** Derbyshire, near Pebley Pond, N of Barlborough, *Blockeel s.n.* (Hb. Blockeel, United Kingdom); Wakefield, near Wintersett reservoir, *Blockeel & Porley s.n.* (Hb. Blockeel 31/418, United Kingdom); Leeds, Temple Newsam, *Blockeel s.n.* (Hb. Blockeel, United Kingdom).

9. Didymodon tophaceus (Brid.) Lisa, Elenc. Musch.: 31. 1837. *Trichostomum tophaceum* Brid., Muscol. Recent. Suppl. 4: 84. 1818 [1819]. *Anacalypta tophacea* (Brid.) Fürnr., Flora 12: 31. 1829. *Didymodon trifarius* var. *tophaceus* (Brid.) Mont., Arch. Bot. (Paris) 1: 140. 1833. *Trichostomum trifarium* var. *tophaceum* (Brid.) Fior.-Mazz., Specim. Bryol. Rom. (ed. 2): 14. 1841. *Barbula tophacea* (Brid.) Mitt., J. Proc. Linn. Soc., Bot. 1: 35. 1859. TYPE: [Germany.] "Comburgi," Feb. 1808, [sine collector] (lectotype, designated here, Hb. Bridel in B!). Figure 2F–I.

Didymodon ceratodonteus (Müll. Hal.) Dixon, Kongel. Norske Vidensk. Selsk. Skr. 1932: 7. 1932. Syn. nov. *Pottia ceratodontea* Müll. Hal., Syn. Musc. Frond. 1: 564. 1849. TYPE: [South Africa.] "Philippstown Katrivier," *C. F. Ecklon s.n.* (lectotype, designated by Magill (1981: 233), BM!).

Didymodon spadiceus var. *siluricus* Velen., Rozpr. České Akad. Věd, Tř. 2, Vědy Mat. Přír. 6: 152. 1897. Syn. nov. TYPE: [Czech Republic.] "Proti Libsicum," Mar. 1893, *J. Velenovský s.n.* (lectotype, designated here, PRC!).

Didymodon tophaceus var. *breidleri* E. Bauer, Lotos 47: 138. 1899. TYPE: [Czech Republic.] "Bohemia centr. Rinnsal gegenüber Libschitz," Aug. 1897, *E. Bauer s.n.* (lectotype, designated here, HBG!; isotypes, GJO!, PR!).

Didymodon bosniacus Glow., Verh. Zool.-Bot. Ges. Wien 56: 196. 1906. TYPE: [Bosnia Herzegovina.] "Bosnien, Pliva-Masserfall bei Zajce," 25 July 1904, *J. Glowacki s.n.* (lectotype, designated here, GJO!).

Didymodon planotophaceus J. Froehl., Ann. Naturh. Mus. Wien 59: 118. 1953. Syn. nov. TYPE: [Iran.] "Prov. Luristan, Bisheh, 50 km a Khorramabad orientem versus, ca. 1200–1400 m," 14–16 July 1948, *K. H. Rechinger 7407* (holotype, S!; isotypes, B!, E!, G!, H!, MO!, NY!, Z!).

Plants 0.3–4(–6) cm high, growing in dense turfs or cushions, olive-green or brown; *stems* erect, simple or branched, central strand differentiated; *rhizoidal tubers* absent. *Leaves* appressed, slightly incurved or patent when dry, erect-patent to spreading, not undulate when moist, lingulate, lanceolate or oblong-lanceolate, not keeled, decurrent at base, (0.3–)0.5–2.2(–3) × (0.15–)0.23–0.8 mm; lamina unistratose, brown-orange or more rarely yellowish with KOH stain; apex obtuse or rounded, sometimes broadly acute and rarely apiculate; margins entire or papillose-crenulate in upper leaf, plane or weakly recurved from base to ½ or ¾ of the leaf; *costa* (30–)50–130(–145) μm wide at leaf base, ending several cells below the apex, very rarely percurrent, ventral cells of the costa in upper leaf elongated, smooth, dorsal cells of the costa in upper leaf quadrate to rectangular, smooth or papillose, in transverse section at leaf base semicircular, with 2 to 6 guide cells in 1 layer, 0 to 2(to 3) layers of ventral stereids, sometimes 1 layer of substereids, 1 to 3 layers of dorsal stereids, with or without ventral epidermis, smooth, dorsal epidermis differentiated, smooth or papillose; *upper and middle laminal cells* subquadrate to irregularly hexagonal, sometimes shortly rectangular, oblate or not, not sinuous, 5–27(–36) × (4–)5–15(–25) μm, with 1 to 2 generally low, sometimes tall, simple or bifurcate papillae per cell, sometimes apparently absent, thick-walled, collenchymatous; *basal cells* rectangular or shortly rectangular, not sinuous, (7.5–)10–75(–100) × (4–)5–15 μm, smooth or papillose, generally thick-walled, not pitted. *Gemmae* in the axils of the leaves absent. *Dioicous. Seta* erect, 0.6–1.9 cm long, red, spirally twisted to left throughout; *capsule* erect or slightly inclined, shortly cylindrical to ovoid, (0.7–)1–2.5 × 0.4–0.86(–1) mm, brown-reddish; *peristome* of 16 teeth irregularly cleft to near base, filiform, papillose, straight, (60–)90–400(–450) μm long, yellowish brown; *operculum* rostrate or long-rostrate, (0.5–)0.7–1.5 mm long; *calyptra* cucullate, 1.2–2.4 mm. *Spores* spherical, 7–18 μm diam., weakly papillose to almost smooth, yellowish brown.

Habitat and distribution. Calcareous rocks or seeping banks by running water that can be occasionally submerged; 0–2900 m; Africa, North America, South America (Churchill et al., 2000), temperate Asia, tropical Asia (Li et al., 2001), Europe. Reported for the first time in Mauritania.

Discussion. The protologue of *Didymodon tophaceus* includes: "in Germania visam clar. Fröhlich Comburgi Suevorum Februario 1808 legit." In Herbarium Bridel at B there are two sheets with the same locality of the original description, but only one shows the date of collection. We select this latter specimen as lectotype.

In the protologue of *Didymodon spadiceus* var. *siluricus*, Velenovský (1897) cited several specimens from different localities. We examined Velenovský's herbarium at PRC in order to locate original material. We found only one specimen whose locality was mentioned in the original description,

so we selected this material as lectotype. The study of this specimen showed that its differential characters are within the usual range of variation of *D. tophaceus*, and it is considered synonymous with the latter species.

In PR, where the original herbarium of Bauer is deposited, we only found a sheet of *Didymodon tophaceus* var. *breidleri*, which belonged to Bauer's *Bryotheca Bohemica* (no. 221). The label matches the locality of the only material mentioned in the protologue; however, the date of collection is later than the publication of this species. On the other hand, we found another specimen collected by Bauer at HBG whose label shows the locality mentioned in the protologue and with a date prior to its publication (August 1827). Therefore, we chose this exemplar as lectotype.

We have studied Glowacki's herbarium at GJO and found two syntypes of *Didymodon bosniacus*. On the label of both specimens was written "Bosnien, Pliva-Masserfall bei Zajce," and they are in total accord with the protologue. We select the specimen marked Nr. 25181/6513 as lectotype since it is better preserved.

Because of the leaf shape, *D. tophaceus* may be confused with *D. luridus* Hornsch., although the papillosity of the lamina cells and the presence of elongate cells on the ventral side of the costa on the upper half of the leaf help distinguish *D. tophaceus* since in *D. luridus* the lamina cells are smooth and the cells of the ventral side of the costa are quadrate.

Didymodon sicculus M. J. Cano, Ros, García-Zamora & J. Guerra is frequently confused with *D. tophaceus*, since they both have the same type of papillosity and apex shape. However, *D. tophaceus* has elongated cells in the ventral side of the costa on the upper half of the leaf, while the cells in *D. sicculus* are quadrate or shortly rectangular. Furthermore, their respective habitats markedly differ, *D. sicculus* being terricolous and growing in dry places, while *D. tophaceus* grows on calcareous rocks over which water runs or in very wet places.

Pottia ceratodontea Müll. Hal. was described by Müller (1849) and was later transferred to *Didymodon* by Dixon as *D. ceratodonteus*, a name that has been widely used in bryological literature (Magill, 1981; O'Shea, 2003). After studying the type material of *P. ceratodontea* we think there are no sufficiently important morphological differences to separate this material from *D. tophaceus*. Therefore, *P. ceratodontea* is proposed as a new synonym of *D. tophaceus*.

Didymodon planotophaceus J. Froehl. was described by Froehlich (1950) from eastern Iran (province of Lorestan) and has not since been collected. According to Froehlich, *D. planotophaceus* is close to *D. tophaceus*, from which it differs by having flat margins and smooth lamina cells. A study of the type material has shown that the same stem may present leaves with both smooth and papillose lamina cells, which is common in *D. tophaceus*. The flat or curved margin also falls within the normal variability of this species. We conclude, therefore, that there are no significant morphological differences between this taxon and *D. tophaceus*, so it should be regarded as being synonymous with the latter.

Side (1983) described the presence of rhizoidal tubers formed of a simple row of cells in several examples from the south of England. Also long leaf structures on the leaf axils, in the form of axillary hairs, and designated teratological axillary hairs, have been described by Allen (1992) in specimens from Arkansas (U.S.A.). These may reach almost three-quarters of the length of the leaves. No type of asexual reproduction was observed in the specimens studied.

Selected specimens examined. ALGERIA. **Algiers:** Philipeville, *Glin s.n.* (S). **Constantine:** prope Constantine, *Appert s.n.* (JE). **M'Sila:** Oasis de Bou Saäda, *Broeksmit s.n.* (L). **Oran:** St. Eugène, *Appert s.n.* (JE). **Tamanghasset:** Zentralsahara, Hoggar Gebirge, Gueltas von Issakarassene, *Frahm s.n.* (MO, NY). **Tizi-Ouzou:** Tizi-Ouzou, *Appert s.n.* (B, JE). EGYPT. **Ad Daqahliyah:** in einem Ausstich bei Matarieh, *Fleischer s.n.* (BP 79949, C, WU, Z). **Al-Wadi Al-Jadid:** Farafra Oasis, *Abou-Salama U-978c* (CAIA). **Alexandria:** Faculty of Science, Alexandria University, *Shabbara s.n.* (CAIA). **Gizeh:** Memphis, *Een s.n.* (S). **Ismailia:** Ismailia, *Een s.n.* (S). **Sinai:** Gebel Saint Katherine, *Abou-Salama U-892b* (CAIA). **Suez:** Eastern Desert, 116 km E of Cairo along the road to Suez, *Een E058* (S). LIBYA. Tripolitania, Bu Gheilam, *Cavara s.n.* (S). MOROCCO. **Fès-Boulmane:** Jbel Bou Iblane, entre el puerto de Tizi-n'Tiskine y Taffert, *Ros et al. s.n.* (MUB 13453). **Taza-Al Hoceima-Taounate:** Jbel Bouhalla, *Cano et al. s.n.* (MUB 10611). MAURITANIA. **Adrar:** barranco de Illij, *González-Mancebo & Ros s.n.* (MUB 14511). AFGHANISTAN. **Bamian:** inter jugum Kota Deraz Kol et Panjao prope pagum Mandigak, *Rechinger 19763* (S). **Helmand:** in der Nähe von Kabul bei Gulbach, *Gilli s.n.* (S). **Kabul:** Band-e-Amir, *Furse & Furse s.n.* (L). ARMENIA. Montes "Karabakhskoie najorge," Goris, in vicinitate pagi vetusbi Khondzoresk, *Vasák s.n.* (GZU). GEORGIA. Borshom pr. fl. Kura, *Brotherus s.n.* (GJO, LE); Imeretia, inter Oni & Utseri, pr. fl. Rion, *Brotherus s.n.* (Z). IRAN. **Gilan:** bei Enseli am Caspischen Meer, *Pichler s.n.* (GJO, WU). **Mazandaran:** Babol, *Starmuahlner s.n.* (S); in valle fluvii Talar inter Abbasabad at Cahi, *Rechinger 2264* (S). IRAQ. **As Sulaymaniyah:** inter Kirkuk et Sulaymaniyah, *Rechinger 15731* (S). **Dahuk:** Solav, Dohuk, *Ráshic s.n.* (E). ISRAEL. **Hazafon:** Upper Galilea, Wadi Karen, *Nachmony 97a* (E). JORDAN. **Al Karak:** Wadi Arava, Fenan in direction to Dana, *Baierle s.n.* (B, Hb. Frey 86–182, Germany). **Irbid:** El-Mashara, *El-Oqlah s.n.* (Hb. Frey 1–4641F, Germany).

SYRIA. **Halab:** Beilan, *Haussknecht s.n.* (BM, JE). TAJIKISTAN. Darvazskogo, p. Odi-Hingou, *Mamatkulov 7392* (LE). TURKMENISTAN. Turkestania, regio Transkaspica, Karakalinsk, *Tschernjekorskaja 435* (GB, LE, S); SW Kopet-Dagh [Mts.], Kara-Kala, *Seyphulin s.n.* (LE). TURKEY. **Adana:** Saimbeyli, *Davis 19889* (E). **Antalya:** ca. 20 km from Manavgat, on road to Ahseki, *Nyholm & Crundwell 1243* (E). **Artvin:** Artvin, *Nyholm 563/74* (S). **Bilecik:** Bilecik, *Bornmüller 13183* (B, HBG, Z). **Denizli:** Honaz Dag, *Walther s.n.* (Hb. Düll). **Khramanmaras:** Taurus Cataonicus, in mote Wank Dagh prope Malatja, *Handel-Mazzetti 2507* (W). **Konya:** near Aksehir Gölü ca. 10 km N Aksehir, *Crundwell et al. 472a/72* (S). **Manisa:** 11 km W of Manisa, *Nyholm 1029/71b* (S). **Mugla:** ca. 2 km E of Cetibeli ca. 13 km N of Marmaris, *Nyholm 487b/71* (S). **Nevseir:** Gülschir und dem kl. Dorf Alkan am SE-Rande des Hirkadag-Massivs, *Becker s.n.* (Hb. Düll). **Ordu:** Vilayet Ordu, Ünye, Black Sea coast, *Rubers 5038* (L). **Sinop:** above the Black Sea shore on the NW side of the Sinop, *Townsend* (Hb. Townsend 88/140, United Kingdom). ALBANIA. **Dürres:** Durazzo, *Kórpáti s.n.* (BP 64449). **Tirana:** Tirana, *Kórpáti s.n.* (BP 64421). AUSTRIA. **Steiermark:** Ennsthal, bei Wölkenstein, *Breidler s.n.* (GJO). **Tirol:** Innsbruck, *Luisier s.n.* (PO 2183). BOSNIA HERZEGOVINA. Kiseljak bei Žepče, *Glowacki s.n.* (GJO, GZU). BULGARIA. **Burgas:** Mt. Strandza, prope Sinemorets, *Petrov s.n.* (SOM). **Khaskovo:** Mt. Rhodope, prope Kardzali, *Ganeva s.n.* (SOM). CROATIA. Dalmatien, bei Makarska sudöstlich von Baskovic, *Froehlich s.n.* (S); Drubrovnik, *Pierrot & Pierrot 73076* (Hb. Pierrot, France). CYPRUS. Kyrenia, *Düll s.n.* (Hb. Düll). FRANCE. **Alpes Maritimes:** La Bocca, dans la Frayere, *Pierrot 55313* (Hb. Pierrot, France). **Ardèche:** Beaulieu, *Jaderholm s.n.* (GB, S). **Bouchês du Rhône:** Aix-en-Provence, Pied de la Sainte Victoire, *Skrzypczak s.n.* (Hb. Skrzypczak 97110, France). **Corse-du-Sud:** Festung Bonifacio an der Südspitze von Korsika, *Hübschmann s.n.* (B). **Deux-Sevres:** Vrines près Thouars, *Biget s.n.* (BCB 1761). **Haute-Corse:** Castirla d'Corde, *Levier s.n.* (S). **Hérault:** Salasc, *Pierrot & Pierrot 92112* (Hb. Pierrot, France). **Ille-et-Vilaine:** Le Vivier, nord for Dol, *Størmer s.n.* (O). **Loiret:** Lettaure, *Thériot s.n.* (S). **Manche:** Cherbourg, *Le Jolis s.n.* (S). **Nord:** Dunkerque, *Lesdain s.n.* (S). **Tarn:** Albi, *Sudre s.n.* (BC). **Var:** Flassans-sur-Issole, *Skrzypczak s.n.* (Hb. Skrzypczak, France). **Vaucluse:** Bonnieux, *Ros s.n.* (MUB 1075). **Vendée:** Les Sables-d'Olonne, *Charrier s.n.* (O). GERMANY. **Bayern:** Friedrichsthale bei Baireuth, *Walther s.n.* (MO). **Hamburg:** bei Bergedorf, *Jaap s.n.* (WU). **Sachsen:** Leipzig, bei Beucha, *Kepsch s.n.* (C). GREECE. **Crete:** Iraklión, 1.5 km oberh. Gonies, Dornstrauch-Shibljak, *Düll s.n.* (Hb. Düll). **Central Greece and Euboea:** Elis, Paralimni, *Rechinger s.n.* (S). **Aegean Islands:** Patmos, on hillside ca. 1 km NW of the harbour of Scala, *Townsend 70/167* (E). **Ionian Islands:** Corfú, bei Nimfes, *Düll s.n.* (Hb. Düll). **Macedonia:** Athos, bei Pródhromos, *Rauh s.n.* (B, JE). **Peloponnese:** Lakonia, Mistras, near Sparti, *Blockeel* (Hb. Blockeel 17/094, United Kingdom). **Thessalia:** *Rechinger 23750* (S). HUNGARY. **Bács-Kiskun:** lacu Szappnszék prope Fülöpháza, *Papp s.n.* (BP 168084). **Budapest:** Budapest, *Boros s.n.* (C, MO). **Jász-Nagykun-Szolnok:** Montes Gyalui havasok, vallis rivi Melegszamos, *Vajda s.n.* (MO). **Liptauer:** Weidengrunde beim Bade Luaski, *Schulz s.n.* (GJO). ITALY. **Abruzzo:** Sanctuario Collelongo, *Düll s.n.* (Hb. Düll). **Calabria:** Catanzaro, *Micheletti s.n.* (BM, C, HBG, JE, M). **Campania:** Fuorigrotta, *Giordano s.n.* (S). **Emilia-Romagna:** presso la fonti nei colli de Sassuolo, *Fiori s.n.* (RO). **Friuli-Venezia Giulia:** Triest, *Haussknecht s.n.* (JE). **Lazio:** Roma, Fontanile ad aqua Traversa, *Cuboni s.n.* (RO). **Liguria:** Zoagli, *Maggio s.n.* (RO). **Lombardia:** Bergamo, Val Gandino, Leffe, *Corti s.n.* (CANM 127401). **Marche:** Piceno, *Orsini s.n.* (RO). **Sardegna:** Tacco di Osimi, *Cogoni s.n.* (Herb Cogoni, Italy). **Sicilia:** Taormina, *Trautmann s.n.* (GB, S). **Toscana:** Gorgonia, *Arcangeti s.n.* (S). **Trentino-Alto Adige:** Castelfondo, prope pontem Novellae, *Evers s.n.* (GZU). **Umbria:** bei Montone, *Hemeyers s.n.* (O). **Veneto:** Tacquitara, Barbargia, *Marcucci s.n.* (JE, M). MACEDONIA. Cerna, *Herzog 644* (JE); Zaduka, *Herzog 638* (JE). MALTA. Buskett, *Mifsud s.n.* (MUB 12542). PORTUGAL. **Algarve:** Lagoa, Senhora da Rocha, Vale do Engenho, *Sérgio et al. s.n.* (LISU 155068). **Alto Alentejo:** Castelo de Vide, Termas de Fadagosa, *Sérgio s.n.* (LISU). **Azores:** S. Miguel, road from Furnas to Ribeira Quente, *Crundwell 1424* (E). **Baixo Alentejo:** Herdade da Ribeira Abaixo, *Garcia s.n.* (LISU 171238). **Beira Litoral:** cerca de S. Bento, *Sérgio s.n.* (COI 169). **Douro Litoral:** Arca de Água, arredores do Porto, *Machado s.n.* (PO 731). **Estremadura:** Aricino, *Machado s.n.* (PO 729). **Madeira:** Deserta Grande, ribeiro do Pedregal, *Nóbrega s.n.* (LISU 162110). **Mihno:** Moledo, *Machado s.n.* (PO 733). **Ribatejo:** Águas-Belas, *Barros s.n.* (LISU 64473). RUSSIA. **Adygeya:** Prov. Kuban, Maikop, *Schapchnikov s.n.* (LE). **North Ossetia:** pr. fl. Ardon, *Brotherus s.n.* (Z). **Krasnodar Kraj:** Khosta, in faucibus fluminis Macesta prope pagum Izmailovka, *Vasák s.n.* (GZU). **Stavropol Kraj:** Kislovodsk Town, *Schteynberg s.n.* (LE). SERBIA AND MONTENEGRO. **Montenegro:** Duboko an der Mrtvica goom, *Glowacki s.n.* (GJO). SPAIN. **Asturias:** Colunga, Playa "La Griega," *Muñoz s.n.* (MA 16438). **Barcelona:** Gavá, *Casas s.n.* (BCB 49825). **Cádiz:** Ronda, *Pierrot & Pierrot 68071* (Hb. Pierrot, France). **Cantabria:** Arnuero, Playa de la Arena, *Muñoz s.n.* (MA 16439). **Castellón:** Ares del Maestre, *Guara s.n.* (VAL 3460). **Córdoba:** Sierra de Córdoba, bei Córdoba, *Fleischer s.n.* (C, M, WU). **Jaén:** Sierra de Segura, Las Acebeas, *Gil s.n.* (GDA 22350). **La Coruña:** Corrubedo, Laguna de Carregal, *Reinoso s.n.* (SANT 2756). **La Rioja:** Anguiano, *García s.n.* (Hb. Martínez-Abaigar, Spain). **Las Palmas:** Fuerteventura, betw. Tetir La Matilla, *Crundwell 1175* (E). **Lérida:** Balaguer, *Casas s.n.* (BCB 37744). **Murcia:** Pliego, Fuente de la Teja, *Ros & Aboal s.n.* (MUB 536). **Santa Cruz de Tenerife:** Tenerife, 1 km E of Puerto de la Cruz, *Crundwell 301* (E, NY). **Teruel:** Alcalá de la Selva, *Varo et al. s.n.* (GDA 13407). SWEDEN. **Jönköping:** Småland, Visingsö, *Arvén s.n.* (WU). **Värmland:** Skane, *Berggren s.n.* (WU). **Växtergötland:** Vestrogothiae, Bellin, *Lindberg s.n.* (WU). SWITZERLAND. **Aargau:** Aarufer bei Brugg, *Geheeb s.n.* (RO). **Tessin:** Bellinzona, *Jäggli s.n.* (GB). UNITED KINGDOM. **England:** Warrington, Yorkshire, *Schimper s.n.* (RO). U.S.A. **Maine:** Knox, Rockport Town, Goose River, *Allen 25750* (MUB 18989).

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TAXONOMIC ADDITIONS FOR *SOLANUM* SECTION *GEMINATA* (SOLANACEAE) IN PERU[1]

Sandra Knapp[2]

ABSTRACT

Two new endemic species of *Solanum* sect. *Geminata* are described from Peru: *Solanum sumacaspi*, from the high-elevation forests in the area around Cusco and Macchu Picchu in southern Peru, and *S. naucinum*, from montane forests around the Yanachaga-Chemillén National Park in the Department of Pasco. *Solanum sumacaspi* had been confused with the Bolivian *S. daphnophyllum* Bitter; its differences from that species are detailed and its species group membership within the section discussed. *Solanum naucinum* is a rare species, similar to a restricted set of other extremely rare taxa (the *Solanum dolosum* species group of Knapp) distributed from Colombia to Bolivia; its differences and key characters are discussed in relation to the *Solanum dolosum* species group of section *Geminata*. The species are illustrated and their conservation status discussed.

Key words: biodiversity, endemic, Peru, protected areas, section *Geminata*, Solanaceae, *Solanum*.

Since the publication of my (Knapp, 2002a) monograph of *Solanum* sect. *Geminata* (G. Don) Walp. (Solanaceae), many new collections from biodiversity-rich regions such as Peru have become available. While examining these, and in the course of preparing the treatment of the endemic Solanaceae of Peru (*Libro Rojo de las Plantas Endémicas del Perú*, B. León, editor, in prep.), new taxa have come to light. Both of these new species occur in or near protected areas managed by Peru's Instituto Nacional de Recursos Naturales, INRENA (<http://www.inrena.gob.pe>), and their recognition and description are important to help conservation efforts in these habitats. Species diversity and endemism in *Solanum* are concentrated at middle to high elevations in the Andes (Knapp, 2002b); these two new taxa confirm this finding.

Species of *Solanum* sect. *Geminata* are difficult to identify using dichotomous keys. The synoptic (multi-entry) key provided in Knapp (2002a: 42–43) is more reliable and useful for identification of these variable and very similar plants. In each of the descriptions below I have suggested where these plants would be inserted in the dichotomous key in each of their respective species groups in the 2002 monograph of *Solanum* sect. *Geminata*, but have also provided the suite of characters that would be used in the synoptic key. Multi-access, synoptic keys are being developed as part of the *PBI Solanum* project (Knapp et al., 2004; see Solanaceae Source, <www.nhm.ac.uk/botany/databases/solanum>, although keys are not yet available) and will be altered as new species are added to the database, thus obviating the need for completely rewriting monograph keys as new taxa are described.

Solanum sumacaspi S. Knapp, sp. nov. TYPE: Peru. Cusco: Urubamba, road from Urubamba to Quillabamba, betw. Ollantaytambo & Abra Malaga, ca. 3500 m, 13°12′15″S, 72°17′49″W, 12 Sep. 2002, *M. Ackermann & D. Kollehn 289* (holotype, USM-179016!; isotypes, BM-000778469!, BSB!, HUSA not seen, M!, NY!). Figures 1, 2A.

Species *Solano daphnophyllo* similis, sed caulibus pallidis flavovirentibus nitidis, inflorescentiis longioribus, pedicellis cicatricibus late dispositis, differt.

Small shrubs to 2 m tall; young stems and leaves minutely and sparsely papillate, soon completely glabrous, pale greenish yellow and shiny, a few (at most 1 or 2) simple uniseriate trichomes sometimes present on very new stems; older stems ridged,

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[2] Department of Botany, The Natural History Museum, Cromwell Road, London SW7 5BD, United Kingdom. sk@nhm.ac.uk.

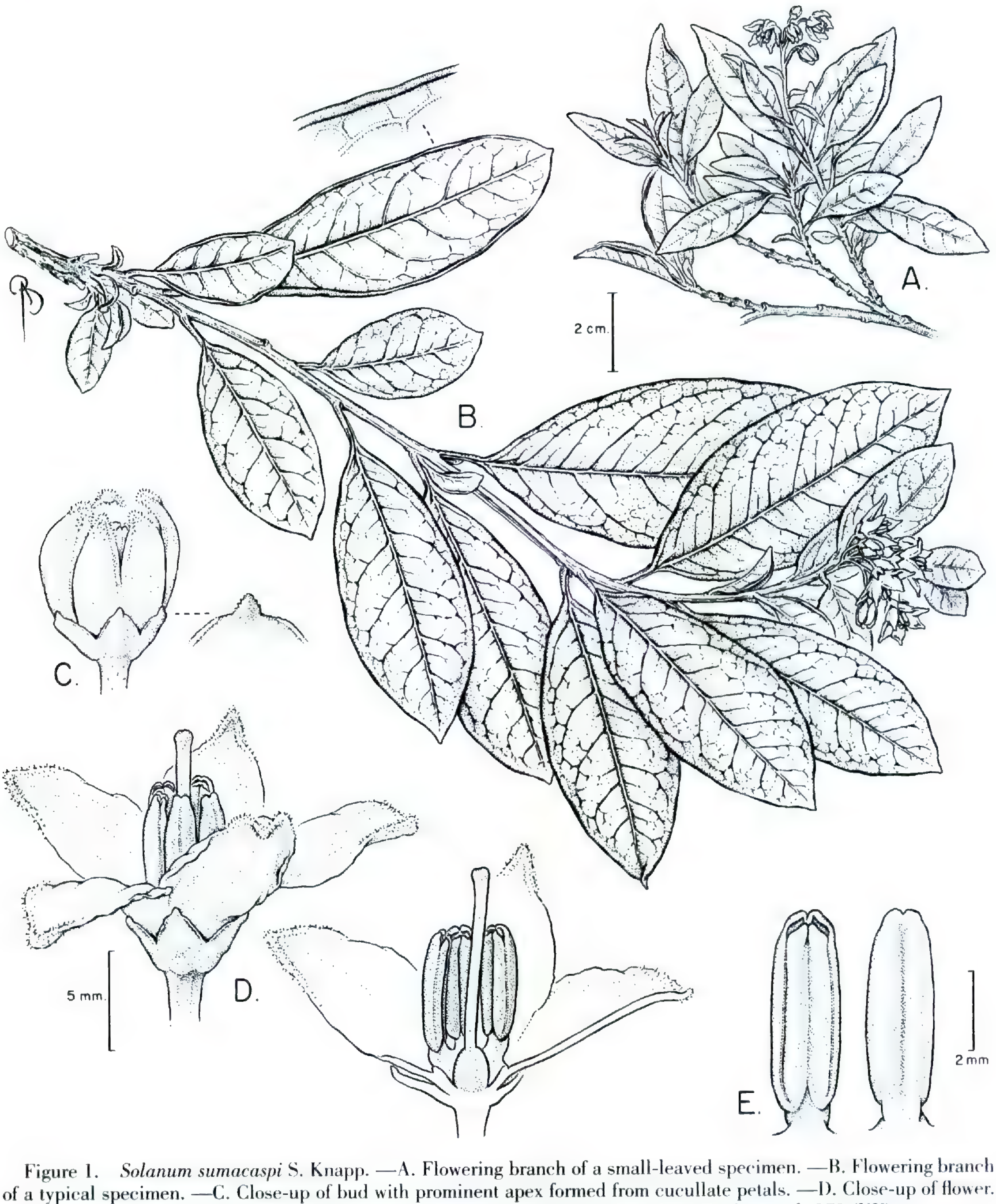

Figure 1. *Solanum sumacaspi* S. Knapp. —A. Flowering branch of a small-leaved specimen. —B. Flowering branch of a typical specimen. —C. Close-up of bud with prominent apex formed from cucullate petals. —D. Close-up of flower. —E. Close-up of anthers. A based on *Valenzuela et al. 1214* (NY); B–E based on *Farfan et al. 373* (NY).

shiny; bark of the older stems and trunks pale greenish white, exfoliating; sympodial units difoliate, apparently geminate, the inflorescences borne at the branch tips and overtopping the leaves. Leaves elliptic, completely glabrous above and below, shiny, thick and fleshy, drying olive green above, pale bright yellowish green below; major leaves 3–11 × 1.3–5 cm, with 5 to 10 pairs of main lateral veins raised and yellowish green above, prominent and bright yellow beneath, the apex acute to somewhat truncate, the base attenuate and decurrent onto the petiole; minor leaves not differing from the major ones in size or shape; petioles 0.1–1 cm long, ridged, the base remaining as a prominent scar on the older stems. Inflorescences opposite the leaves, simple, 1–2 cm long, (4- to)7- to 10-flowered, glabrous and shiny; pedicel scars widely spaced ca. 2 mm apart, the pair of scars

closer than the distance between the scar pairs, flowers borne from near the base of the inflorescence; pedicels at anthesis 0.5–1 cm long, somewhat deflexed, tapering from the abrupt base of the calyx tube to a slender base 0.5–0.8 mm diam., green and shiny. Buds, when very young, appearing globose, the corolla soon exserted from the calyx lobes, the buds later becoming ellipsoid just before anthesis; flowers with the calyx tube 0.9–2 mm long, broadly open and conical, the lobes 2–2.5 mm long, deltate to rounded, glabrous, the margins thickened and drying white, the tip with a thickened mucro ca. 1 mm long (which may be swollen in fresh material), the mucro occasionally notched; corolla 1.4–2.5 cm diam., white or cream-colored, lobed nearly to the base, the lobes planar or somewhat campanulate at anthesis, glabrous on both surfaces, the tips of the lobes minutely papillose and somewhat cucullate; free portion of the filaments ca. 1 mm long, the filament tube ca. 0.25 mm long to absent; anthers 5–6 × 1–1.5(–2) mm, poricidal at the tips, the pores teardrop-shaped, the tips thickened and paler; ovary glabrous; style straight, 1–1.2 cm long; stigma capitate, green. Fruit not known; seeds not known.

Etymology. From the Quechua *sumaj* = beautiful, *caspi* = shrub, referring to the striking shiny foliage and large showy inflorescences of this species. Since this species epithet is arbitrarily taken from the Quechua language, its spelling is to be maintained (cf. Art. 23.2, ICBN; Greuter et al., 2000).

Distribution. In high-elevation secondary forests near steppeland in southern Peru, from 2100 to 3400 m, most collections from the Río Urubamba drainage in the province of Urubamba, Cusco.

In the monograph of *Solanum* sect. *Geminata* (Knapp, 2002a) I included the Peruvian collections *Peyton & Peyton 147, 1026 & 1026b* and *Ferreyra 16683* in the delimitation of *Solanum daphnophyllum* Bitter, a similarly glabrous species from Bolivia, but with some reservations. Recent collecting in the high-elevation steppelands and forests in the Department of Cusco resulted in several additional collections, confirming the distinctness of *S. sumacaspi*, both morphologically and in habitat. The collection from the Department of Puno (*Ferreyra 16683*, MO, USM) does represent *S. daphnophyllum* (Knapp, 2002a), but material from the Cusco area does not. *Solanum daphnophyllum* is a species of middle to high elevation (700–2800 m) dry to semi-humid forests on the eastern Andean slopes from central Bolivia to the Department of Puno in Peru (*Ferreyra 16683*), while *S. sumacaspi* is apparently only found in disturbed forests in much higher elevations (2100–3500 m) in grassland (puna)/forest transition areas in the Urubamba River drainage. Morphologically, *S. sumacaspi* differs from *S. daphnophyllum* in its more elongate inflorescences with more widely spaced pedicel scars and in its pale green, exfoliating bark; *S. daphnophyllum* has inflorescences usually only ca. 1 cm long, and dark reddish shiny bark on all stems. The apparently geminate sympodial units also differentiate *S. sumacaspi* from *S. daphnophyllum*, which has difoliate, but not geminate, units.

Fruiting material is lacking for *Solanum sumacaspi*, preventing its firm allocation to one of the putative species groups of section *Geminata* (Knapp, 2002a). Should the seeds be flattened reniform, *S. sumacaspi* is likely to be a member of the *Solanum nudum* species group (sensu Knapp, 2002a), and would key out in the first set of couplets, either with *S. restingae* S. Knapp and *S. warmingii* Hiern (both of southeastern Brazil) or with *S. daphnophyllum* Bitter and *S. cordioides* S. Knapp. *Solanum sumacaspi* differs from the first two in its unwinged stems and deltate calyx lobes and from the second pair by the characters detailed above with discussion of *S. daphnophyllum*. *Solanum cordioides*, an endemic species of southeastern Brazil, has a highly branched inflorescence with tiny greenish white flowers and could not be confused with *S. sumacaspi*.

Solanum sumacaspi also morphologically resembles two species in the *Solanum arboreum* species group (sensu Knapp, 2002a) in its showy inflorescences of flowers all apparently opening at once; *S. gratum* Bitter of the Cordillera de la Costa in Venezuela and *S. plowmanii* S. Knapp of the western Andean slopes in Peru and Ecuador. The shiny stems also are similar to *S. goniocaulon* S. Knapp of the eastern Andean slopes of northern Peru and southern Ecuador, also of the *S. arboreum* species group. It can be differentiated from all those species by the combination of its yellowish exfoliating bark, shiny leaves that dry a very pale green, its non-anisophyllous leaves and its high-elevation southern Peruvian distribution.

The following suite of characters from the synoptic key in Knapp (2002a: 42–43) will differentiate *S. sumacaspi*: bark of older stems exfoliating; plants completely glabrous; and possibly calyx lobes orbicular (live plants; see Fig. 1C; otherwise only known in the Costa Rican species *S. pastillum* S. Knapp). The distribution and high-elevation habitat of *S. sumacaspi* would further differentiate it from other superficially similar species.

Since *Solanum sumacaspi* appears to be relative-

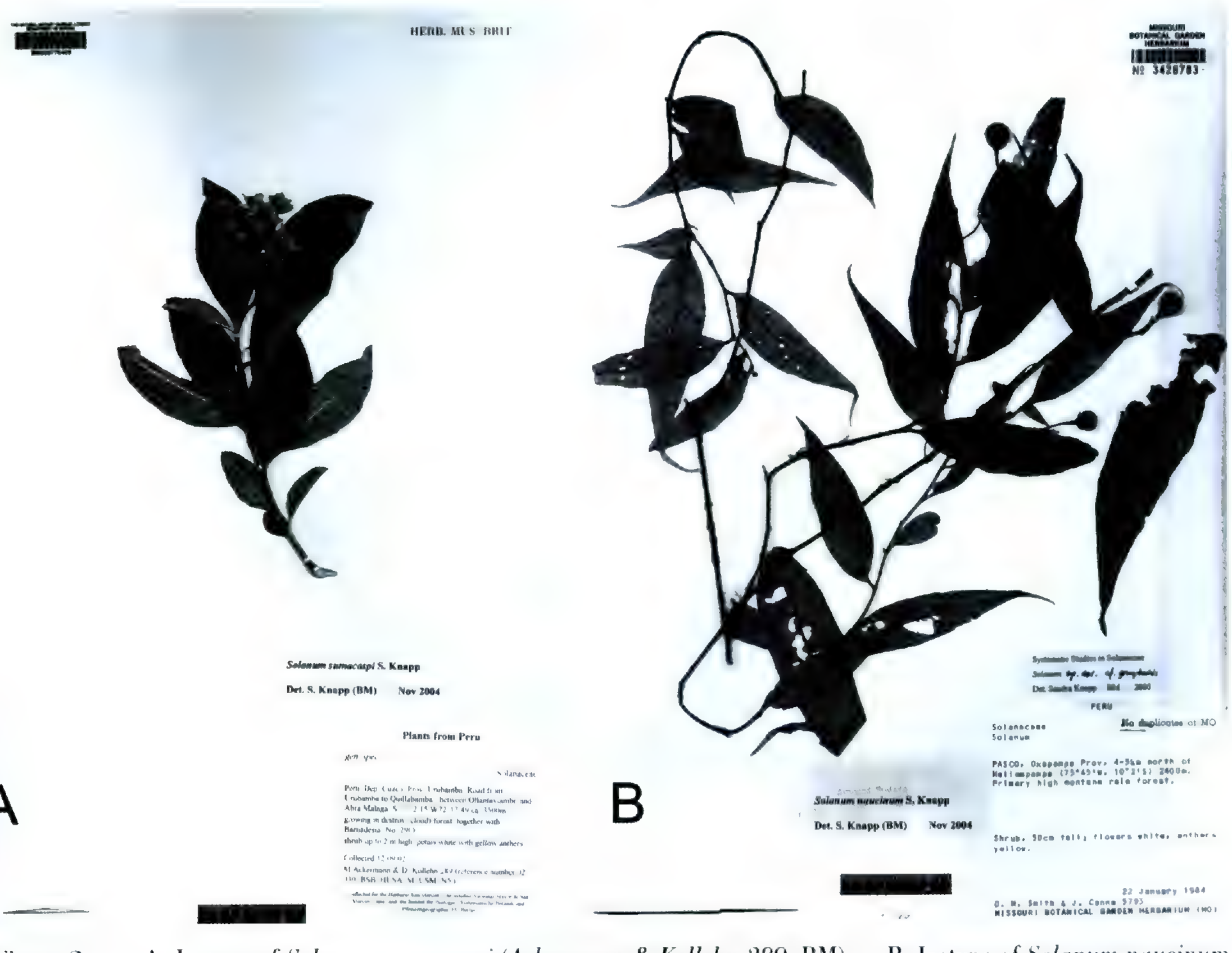

Figure 2. —A. Isotype of *Solanum sumacaspi* (*Ackermann & Kollehn 289*, BM). —B. Isotype of *Solanum naucinum* (*Smith & Canne 5793*, MO).

ly common in the Cusco area, fruiting collections are a priority in order to assign it to a species group with confidence. DNA sequence studies under way on a genus-wide scale in *Solanum* (Bohs, 2005) will certainly, however, lead to reassessment of these informal species groups based only on overall morphology.

Solanum sumacaspi occurs in the ecotone between the Peruvian puna (Young et al., 1997) and eastern slopes of the Peruvian Andes centers of plant diversity. These habitats in southern Peru are generally drier than similar grassland to forest transition zones further to the north, and often experience a marked dry season (Young et al., 1997). Specimens of *S. sumacaspi* have been collected in or near the Santuario Histórico Macchu Picchu, an area with some protection from human intervention, although pressure on forests of these types from overgrazing can be severe (Kok et al., 1995; Young et al., 1997). However, most specimens appear to come from secondary or disturbed forest and forest edges, indicating either that this species is a colonizer or that the forest is highly disturbed and impacted. The conservation status of *S. sumacaspi* has not been formally evaluated, as no information as to population size is included on labels, but it is likely to be not at immediate threat, based on its recent collection and its apparently secondary growth habitat.

Paratypes. PERU. **Cusco:** Urubamba, Ollantaytambo, Huaytampo, *G. Calatayud, I. Huamantupa, J. Farfán, R. Cheverria & T. Blanco 966* (BM, CUZ not seen, MO, NY, USM), *J. Farfán, F. Carazas, O. Farfán & E. Urquiaga 373* (BM, CUZ not seen, HUT not seen, MO, NY, USM not seen); Urubamba, Yucay, Huaran, *J. Farfán & A. Tupayachi 424* (CUZ not seen, MO, NY, USM not seen); Urubamba, Macchu Picchu, above town of Pauqarcancha, *B. Peyton & S. T. Peyton 147* (MO); Urubamba, Macchu Picchu, along Inca trail in Tres Piedras Blancas, 1 km from Huayabamba, *B. Peyton & S. T. Peyton 1026, 1026b* (MO); Calca, Lares, Manto, *L. Valenzuela, E. Suclli, I. Huamantupa & J. Farfán 1214* (CUZ not seen, MO, NY).

Solanum naucinum S. Knapp, sp. nov. TYPE: Peru. Pasco: Oxapampa, 4–5 km N of Mallampampa, 2400 m, 10°02′S, 75°45′W, primary high montane rain forest, 22 Jan. 1984, *D. M. Smith & J. Canne 5793* (holotype, USM-146535!; isotype, MO-3428783!). Figure 2B.

Species *Solano gonyrhachidi* affinis, sed foliis pubescentibus trichomatibus fulvis dendriticis erectis, calycibus lobis longiore triangulatis, differt.

Small shrub to 50 cm; young stems and leaves densely golden pubescent, the trichomes 0.5–1 mm, dendritic, uniseriate with single-celled branches; older stems glabrescent, thin and flexuous; bark of the older stems pale brown; sympodial units unifoliate, occasionally difoliate and geminate on non-reproductive nodes. Leaves 7–15 × 1.5–3.2 cm, narrowly elliptic to narrowly oblanceolate or lanceolate, glabrous adaxially, pubescent abaxially on the veins and lamina with golden uniseriate dendritic trichomes to 1.5 mm, the trichome branches unicellular, pubescence denser along the veins, with 8 to 11 pairs of primary veins, these looping to form a distinct marginal vein, the apex long-acuminate, blunt at the extreme tip, the margins entire, slightly revolute, the base acute, sometimes somewhat oblique; minor leaves on non-reproductive nodes smaller, but similar in shape to the major leaves; petioles 0.3–0.6 cm, densely pubescent. Inflorescences opposite the leaves, simple, 5–8 cm, 8- to 10-flowered, densely pubescent with golden dendritic trichomes to 1 mm; pedicel scars spaced 2–4 mm apart, beginning ca. 1 cm from base of inflorescence. Buds not seen; flowers white (fide *Smith & Canne 5793*), not seen. Fruit ca. 1 cm diam., a globose, green (immature?) berry, drying mustard yellow on herbarium specimens; fruiting pedicels 1–1.2 cm, pendent, ca. 1 mm diam. at the base, ca. 2 mm diam. at the apex; calyx lobes in fruit ca. 3 mm, long-triangular, pubescent with golden dendritic trichomes; seeds not mature in fruit examined, ovoid-reniform to slightly flattened, ca. 3 × 2 mm, the surfaces minutely pitted, the margins not incrassate.

Etymology. *Naucinum* refers to the Latin for trivial, recognizing the inconspicuous and overlooked nature of this plant.

Distribution. Only known from the type specimen collected in the montane forests of the Cordillera de Yanachaga (near Parque Nacional Yanachaga-Chemillén) in the Department of Pasco, Peru, at about 2400 m.

Solanum naucinum is a member of the *Solanum dolosum* species group (sensu Knapp, 2002a), with unifoliate sympodia on reproductive nodes, filamentous inflorescences and long-acuminate leaves with ciliate margins near the apex. It differs from all other species in the group in its distinctive golden dendritic pubescence. Like the other taxa in the *S. dolosum* species group (Knapp, 2002a), *S. naucinum* is apparently a rare plant. I listed the type collection of *S. naucinum* in the monograph of section *Geminata* (Knapp, 2002a) as a probable new species, but no new specimens have come to light and I feel it is, despite the relatively fragmentary material, useful to describe the species in order that other botanists will know what to look for and perhaps collect it again. *Solanum naucinum* shares with *S. gonyrhachis* an elongate inflorescence with widely spaced pedicel scars. In the key to the *S. dolosum* species group an additional couplet could be added: plants with dendritic pubescence (*S. naucinum*) versus plants with simple uniseriate pubescence or glabrous (*S. dolosum* C. V. Morton of Colombia and Ecuador, *S. gonyrhachis* S. Knapp of Bolivia, *S. habrocaulon* S. Knapp of northern Peru). Characters from the synoptic key useful for differentiating *S. naucinum* are: unifoliate sympodia; dendritic trichomes; pagoda-like architecture (sensu Knapp, 2002a); and a filiform inflorescence.

Like its close relatives, *Solanum naucinum* is a spindly shrub, possibly also growing as a hemiepiphyte in its cloud forest habitat. Seeds in the fruits on the type specimen are immature, but appear to be ovoid-reniform without incrassate margins; however, mature fruits and flowers are needed to complete the morphological description of this rare species. Although this material is limited for the description of a new taxon, no new collections of this rare species have come to light in the past 20 years. By describing *S. naucinum*, I hope to stimulate botanists to look for it as collecting intensifies in these biodiversity-rich regions of eastern Peru. Unless species are described they cannot be used as either units for listing or as identifiable targets for conservation action on the ground (see Mace, 2004) and thus become outside scientific analysis.

The type of *Solanum naucinum* was collected within or very near to what was designated the Parque Nacional Yanachaga-Chemillén in 1986 (INRENA, <http://www.inrena.gob.pe/>), a relatively undisturbed region in the Upper Pachitea River drainage of the eastern slopes of the Peruvian Andes (Young, 1992, León & Young, 1997). Edaphic diversity in the park may account for its high floristic diversity (R. B. Foster cited in Young et al., 1997): it sits on the transition zone between two major geological areas of the Andes. The Parque Nacional Yanachaga-Chemillén is very inaccessible, perhaps affording it some protection from large-scale coca cultivation, the principal cause of habitat destruction in this center of plant diversity (Henkel, 1995; Young et al., 1997); however the inaccessibility of these areas, both outside and within the park, may also make them more attractive to illegal coca growers. *Solanum naucinum* is of uncertain conservation status: our knowledge is limited due to lack of collections. It is likely to be

vulnerable due to low population size and restricted range.

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THE *STENOBASIPTERON WIEDEMANNI* (DIPTERA, NEMESTRINIDAE) POLLINATION GUILD IN EASTERN SOUTHERN AFRICA[1]

C. J. Potgieter[2] *and T. J. Edwards*[2]

Abstract

Stenobasipteron wiedemanni, a long-proboscid nemestrinid fly, services a Guild of flowers distinct from the *Prosoeca ganglbaueri* pollination Guild in which it has previously been placed. The former fly is the recorded pollinator of 19 plant species in six families: the Acanthaceae, Balsaminaceae, Gesneriaceae, Iridaceae, Lamiaceae, and Orchidaceae. *Stenobasipteron wiedemanni* is a mainly forest-dwelling fly with a proboscis length of 19–30 mm. The plant species that are pollinated by this fly are also restricted to forest (or woodland) habitat along the eastern parts of southern Africa. The flowers of plants in this pollination Guild tend to have long, narrow nectaries and corollas in shades of purple, pink, mauve, pale blue, and white. Nectar is present in all species, pollination is diurnal, and most species have zygomorphic flowers with nectar guides. This pollination Guild is separated on the basis of the limitation of the fly, *S. wiedemanni*—and hence the plant species—to forest or closed-canopy habitat. Biogeographically, the *S. wiedemanni* Guild also occurs at lower altitudes in subtropical regions of southern Africa.

Key words: Acanthaceae, *Asystasia*, Balsaminaceae, *Barleria*, *Brownleea*, forest, Gesneriaceae, *Hesperantha*, *Hypoestes*, *Impatiens*, Iridaceae, *Isoglossa*, Lamiaceae, long-proboscid flies, Nemestrinidae, Orchidaceae, *Plectranthus*, pollination, *Stenobasipteron wiedemanni*, *Streptocarpus*.

The study of long-proboscid fly pollination is a subject of increasing interest in southern Africa. This pollination syndrome is well represented on the sub-continent and has been reported for a number of plant families: Ericaceae (Rebelo et al., 1985), Iridaceae (Goldblatt et al., 1995; Goldblatt & Manning, 1999; Manning et al., 1999), Orchidaceae (Johnson & Steiner, 1995, 1997), Geraniaceae (Struck, 1997), and Lamiaceae (Potgieter et al., 1999; Potgieter & Edwards, 2001). This pollination syndrome was reviewed by Goldblatt and Manning (2000), and three discrete Guilds were identified. These are the *Prosoeca peringueyi* Guild, the *Moegistorhynchus–Philoliche* Guild, and the *Prosoeca ganglbaueri* Guild.

The *Prosoeca peringueyi* Guild is restricted to the western half of the winter-rainfall area in southern Africa and comprises two fly species that pollinate flowers with intense shades of violet, deep purple, and magenta, often with cream to yellow markings and areas of darker pigmentation (Goldblatt & Manning, 2000). The *Moegistorhynchus–Philoliche* Guild comprises six to seven species of nemestrinid and tabanid flies, the tabanids extending from southern Namibia to southeastern parts of the Western Cape (see Fig. 1 for location of provinces in South Africa), with the nemestrinids being restricted to narrow ranges in the southwestern parts of the Western Cape. Flowers in this second Guild are white to cream with pink undertones, or pale to deep pink; nectar guides are red or deep pink (Goldblatt & Manning, 2000). These two Guilds occur in the winter-rainfall areas of southern Africa, while the *Prosoeca ganglbaueri* Guild (in which *Stenobasipteron wiedemanni* has been placed) occurs mainly in summer-rainfall areas.

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[2] School of Botany & Zoology, University of KwaZulu-Natal, Pietermaritzburg, P/Bag X01, Scottsville, 3209, KwaZulu-Natal Province, South Africa. potgieterej@ukzn.ac.za.

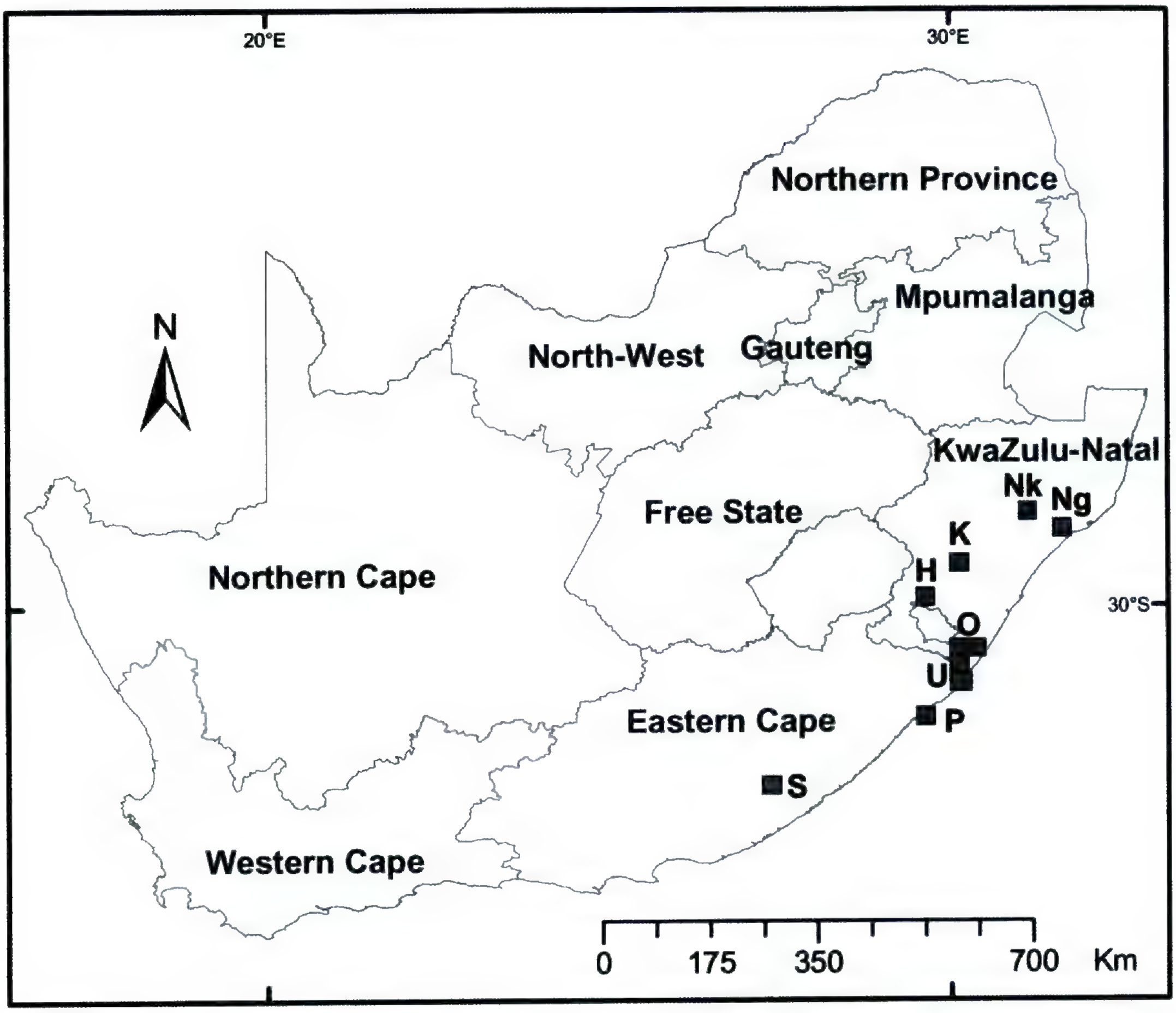

Figure 1. Map of South Africa showing provinces and study sites. Note that Northern Province is now called Limpopo Province. —Nk. Nkandla Forest. —Ng. Ongoye Forest. —K. Karkloof (Leopards Bush Nature Reserve). —H. Hlabeni Forest (Creighton). —O. Oribi Gorge Nature Reserve. —U. Umtamvuna Nature Reserve. —P. Port St. Johns. —S. Stutterheim (Kologha Forest).

The *Prosoeca ganglbaueri* Guild sensu Goldblatt and Manning (2000) included four nemestrinid fly species: *Prosoeca ganglbaueri* Lichtwardt, *Prosoeca longipennis* Loew, *Prosoeca robusta* Bezzi, and *Stenobasipteron wiedemanni* Lichtwardt. Of these species, the floral Guilds pollinated by the first three show considerable overlap, but no overlap has been shown with the Guild pollinated by *S. wiedemanni*. Flowers pollinated by the first three fly species are pink with dark pink markings, but some species are cream or white or deep blue. The fourth fly species, *S. wiedemanni*, visits flowers in shades of pink, pale blue, or mauve (Goldblatt & Manning, 2000). Goldblatt and Manning (2000) indicated that further research may show this latter species to constitute a separate Guild of pollinating flies, and in this paper we confirm the existence of this separate *S. wiedemanni* pollination Guild.

Stenobasipteron wiedemanni (cited as *Stenobasipteron* sp. in Potgieter et al., 1999) is a brown nemestrinid fly species with a proboscis length of 19–30 mm. The species is largely limited to subtropical and temperate forests along the eastern seaboard of southern Africa (Potgieter & Edwards, 2001), and adults have been collected from December to June, with activity in each locality restricted to a few months during summer (see Appendix 1). By contrast, the nemestrinid genera *Moegistorhynchus* and *Prosoeca* occur in temperate fynbos, montane grasslands, and other habitats without a closed canopy.

We proposed (Potgieter & Edwards, 2001) that there are a number of long-tubed species in genera of Lamiaceae in South Africa that are pollinated by either *Stenobasipteron* or *Prosoeca*, depending on habitat. Comparative plant and long-proboscid fly pollinator distributions are presented in Potgieter and Edwards (2001). These species are distributed over the eastern part of the country and include long-tubed members of *Plectranthus* (Potgieter et al., 1999), *Hemizygia*, *Salvia*, *Stachys*, *Orthosiphon*

(Goldblatt & Manning, 1999, 2000), and *Thorncroftia*. Goldblatt and Manning (2000) included species of *Thorncroftia* as inferred members of their *Prosoeca ganglbaueri* Guild.

In forests of the eastern seaboard of southern Africa a number of plant families have evolved long, narrow corolla tubes, spurs, or hypanthia (ca. 20–35 mm), and in our study area we suggest that *Stenobasipteron wiedemanni* may be the primary pollinator of such species. Most of these plant species are unscented and have flowers of mauve, pink, purple, pale blue, or white.

Materials and Methods

Fieldwork was conducted during the main flowering season of *Plectranthus*, between December and May, from 1995 to 2002. Study sites for pollinator observations are shown in Figure 1. We avoided over-collecting fly specimens, since the species occurs at low densities and we did not want to impact on the pollination service it renders. Where appropriate, observations of insect visits were followed by capture of voucher specimens that were killed in separate ethyl-acetate-containing vials and pinned with proboscides extending forward for easy measurement. Areas of pollen deposition were identified under a dissecting microscope, and samples of pollen were collected using blocks of Fuchsin Jelly and mounted. Slides were studied with a compound light microscope, and pollen samples were identified by comparison with reference slides of pollen from plants flowering in the area.

Stenobasipteron wiedemanni is not easily confused with other insects in the study area, and thus only one (or rarely a few) vouchers were collected per plant species to ascertain areas of pollen deposition on the insect. After the first voucher per plant species was captured, careful observations of flies during subsequent flower visits allowed the observer to judge whether pollen would be deposited on certain areas of the insect.

In cases where observations were not made by the authors of this paper, we relied on personal communication with other field workers that obtained photographic records or insect vouchers where possible.

Insect vouchers for this study are lodged with the Natal Museum in Pietermaritzburg, South Africa, and plant vouchers are housed at NU, Natal University Herbarium (see Appendices 1 & 2).

Distributions of the fly species were compiled from field observation and by using data from the Natal Museum (Pietermaritzburg), Albany Museum (Grahamstown), and the South African Museum (Cape Town).

Distributions of Guild constituents were compiled from NU and PRECIS (National Herbarium, Pretoria (PRE) Computerised Information System), as well as published information (Codd, 1985; Pooley, 1998; Linder, 1981; Hilliard & Burtt, 1986; Edwards, 1988) and observations made during the course of this study. Distribution maps for shorter-tubed species of *Plectranthus* are available in Potgieter et al. (1999).

Distribution maps were generated using ArcGIS, combining data from MS Access. Data were collected at quarter-degree-grid level, and hence the forest land cover was re-sampled to quarter-degree-grid resolution.

Floral and other characters of plants shown to be effectively visited by *Stenobasipteron wiedemanni* were compared, and these data were used to suggest other possible members of the Guild.

Nectar volume measurements were made during mornings from cultivated plants in a greenhouse, and these represent the maximum amount of nectar available to insect visitors. Nectar concentrations (as percentage of sucrose equivalents) were measured using a Bellingham & Stanley Eclipse (0–50%) hand-held refractometer. Nectar samples were dried on Whatmans no. 1 filter paper and analyzed using a modified Gas Chromatographic nectar sugar analysis method based on Tanowitz and Smith (1984). Samples of 10 to 30 flowers were pooled to obtain sufficient nectar for analysis.

Results

The Pollinator

Stenobasipteron wiedemanni is a day-flying dipteran that visits flowers from about 9 A.M. to 4 P.M., extracting nectar as a reward. Specimens have been collected between December and July, but we found that in the Eastern Cape and KwaZulu-Natal activity continued to about May (depending on the year).

The behavior of these flies makes them ideal pollinators of long-tubed flower species. During flight the proboscis is folded underneath the body, but as a flower is approached the proboscis is brought forward to extend in front of the body (Fig. 2A). Flies hover in front of flowers while probing for nectar, but occasionally grasp protruding filaments or styles (in the case of Lamiaceae) or rest on landing platforms (e.g., in *Isoglossa hypoestiflora* Lindau, Acanthaceae). Visits to individual flowers last between one and four seconds, and a number of flowers on the same inflorescence or plant may be

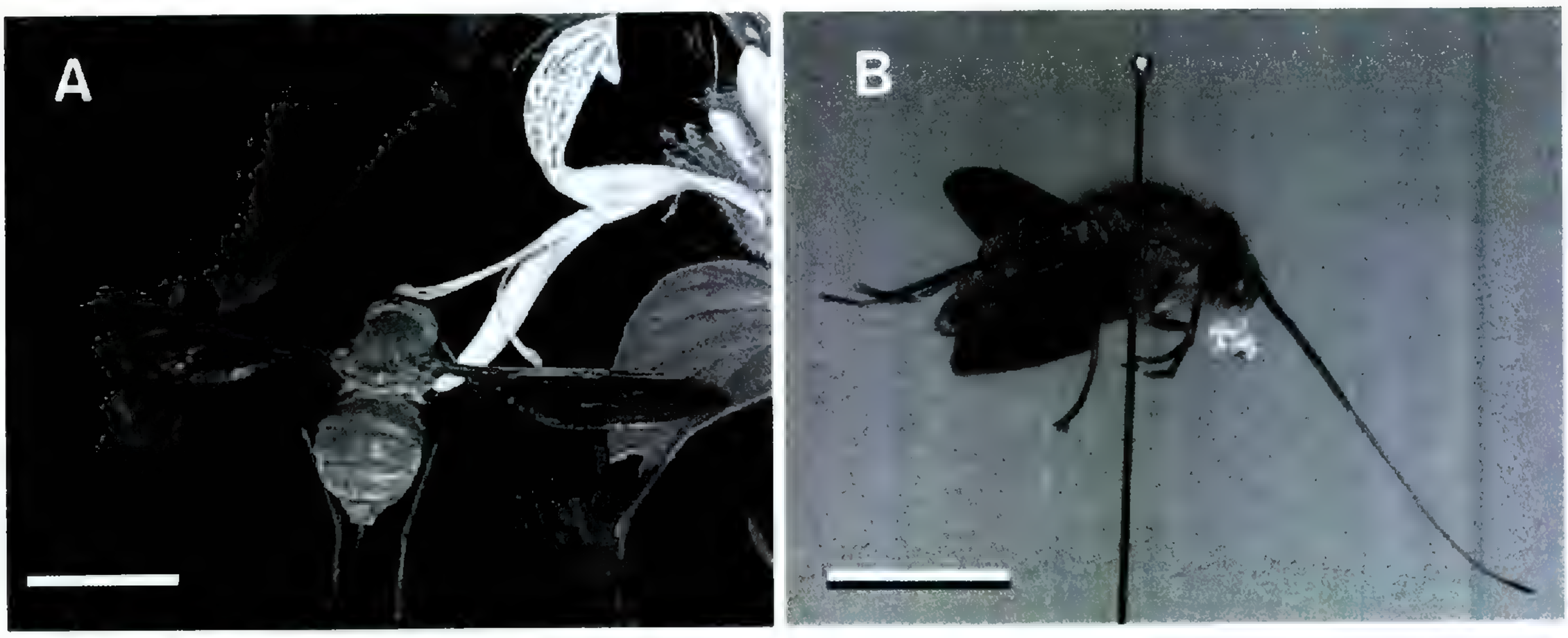

Figure 2. —A. *Stenobasipteron wiedemanni* visiting a flower of *Hypoestes aristata*. The proboscis is extended forward and upward on approach of the flower. —B. *S. wiedemanni*, with pollinaria of *Brownleea coerulea* attached to the base of the proboscis. This specimen also carried pollen from *Isoglossa hypoestiflora* on the dorsal surface, from *Hesperantha huttonii* on the face and from *Plectranthus* on the ventral surface. Scale bars 10 mm.

probed sequentially. The flies are highly mobile, strong fliers that can cover large distances in the forest understory. This is evident from the fact that we observed low frequency visitation at individual patches of studied plants. The relatively large body size (up to 20 mm long, excluding proboscis) offers many sites for pollen deposition (Fig. 2B).

THE FLORAL GUILD

Nineteen species from six plant families are currently included in the *Stenobasipteron wiedemanni* pollination Guild (Table 1). Members of this Guild have functional floral tube lengths that range from 16 to 39 mm (Table 1). This length coincides with that of the proboscis of *Stenobasipteron wiedemanni* (19–30 mm). Shorter-tubed species that also belong to the Guild have tube lengths of 6–21 mm, but often have filaments that approach the length of the long-tubed species (indicated by ' in Table 1). *Plectranthus saccatus* Benth. contains forms with variable corolla tube length, hence the emphasis on the long-tubed forms relevant to this study.

Flowers of species that belong to this Guild are zygomorphic with flowers held horizontally, and where they tend to be more actinomorphic (e.g., *Hesperantha*), the floral tubes are held horizontally. Pollinators are thus directed to visit in a certain way. Nectar guides are present in many of the species.

DISTRIBUTION OF THE GUILD

The distribution of *Stenobasipteron wiedemanni* coincides with the Forest Biome along the eastern seaboard of South Africa (Fig. 3A). Similarly, members of the Guild coincide with forest and fly distribution (Figs. 3, 4). The presence of *S. wiedemanni* at Ongoye Forest, Oribi Gorge Nature Reserve (N.R.), Umtamvuna N.R., Ngeli Forest, Hlabeni Forest (Creighton), Hlatikhulu Forest, and Port St. Johns is based on new distribution records resulting from this study.

The maps only include South Africa (excluding Swaziland and Mozambique), but it is likely that the fly distributions, and that of some of the plant species involved in the Guild, extend into these neighboring countries.

FLOWER-POLLINATOR INTERACTION

A comparison of areas of pollen deposition on *Stenobasipteron wiedemanni* shows that few of the long-tubed plant species share the same site on the insect (Fig. 5 and listed in Table 1). In cases where this does happen, the plants do not co-occur (except in a case of two *Plectranthus* species at one of the study sites). Even though we did not study *Orthosiphon tubiformis* R. D. Good, we included it in Figure 5 to show where pollen would be deposited on the insect. It shares the same areas of deposition on the insect as long-tubed *Plectranthus* species, but is allopatric.

Nectar volumes range from 0.1 to 8.7 µl per flower with high maximum volumes found in the longer-tubed species (Table 2). Nectar sugar concentrations range from 24% to 33% sucrose equivalents (Table 2), which falls within the range reported by Goldblatt and Manning (2000). Nectar tends to be sucrose dominant, i.e., sucrose:hexose ratio > 1 (Table 2), with two species having sucrose

Table 1. Floral and other characters of plants pollinated exclusively or partially by *Stenobasipteron wiedemanni* (the "fly"). In five *Plectranthus* species with short and medium tubes, as well as in *Hypoestes aristata* (indicated with [1]), the style and stamen filament lengths approach that of the tube lengths of long-tubed species. F = forest, W = high-altitude open woodland/wooded savanna. [2] = narrow portion of floral tube, where tube length is longer, but sufficiently broad distally to allow access to a fly or bee body. See Appendix 2 for references for floral tube lengths and pollinator observations.

Plant species (arranged by family)	Habitat	Flower color	Length of floral tube spur (mm)	Area of pollen deposition on fly	Is the fly the only observed visitor to reach nectar?
Lamiaceae					
Plectranthus ambiguus	F	pinkish purple	20–33	ventral thorax & abdomen	yes
P. hilliardiae	F	pale mauve	21–32	ventral thorax & abdomen	yes
P. reflexus	F	pale blue	24–30	ventral thorax & abdomen	no
P. saccatus (long-tubed)	F	mauve to pale blue	20–30	ventral thorax & abdomen	yes
[1]*P. ecklonii*	F	bluish purple	10–15	ventral head & thorax	no
[1]*P. zuluensis*	F	pale/dark blue	12–13	ventral head & proboscis base	no
[1]*P. ciliatus*	F	white	6–8	proboscis	no
[1]*P. fruticosus*	F	bluish mauve	6–9	ventral head & thorax	no
[1]*P. praetermissus*	F	blue to purple	13–15	proboscis	no
Orthosiphon tubiformis	W	pale pink	20–36	ventral thorax & abdomen	yes
Acanthaceae					
Isoglossa hypoestiflora	F	mauve	24–27	dorsal thorax	yes
[1]*Hypoestes aristata*	F	bright pink	11–21	ventral thorax & abdomen	no
Barleria obtusa	F edge	blue to purple	[2]12–18	ventral & lateral thorax	no
Orchidaceae					
Brownleea coerulea	F	mauve	20–24	base of proboscis	yes
Balsaminaceae					
Impatiens hochstetteri subsp. *hochstetteri*	F	pink	(10–)16–24(–27)	proboscis	no
Gesneriaceae					
Streptocarpus formosus	F	pale violet	[2]31–36	dorsal body	yes
Iridaceae					
Hesperantha brevicaulis	—	pink	25–37	—	—
H. huttonii	F	purple	22–27; 33–39	ventral & lateral head & thorax	no
Gladiolus macneilii	W	pink	[2]32–37	dorsal thorax	yes

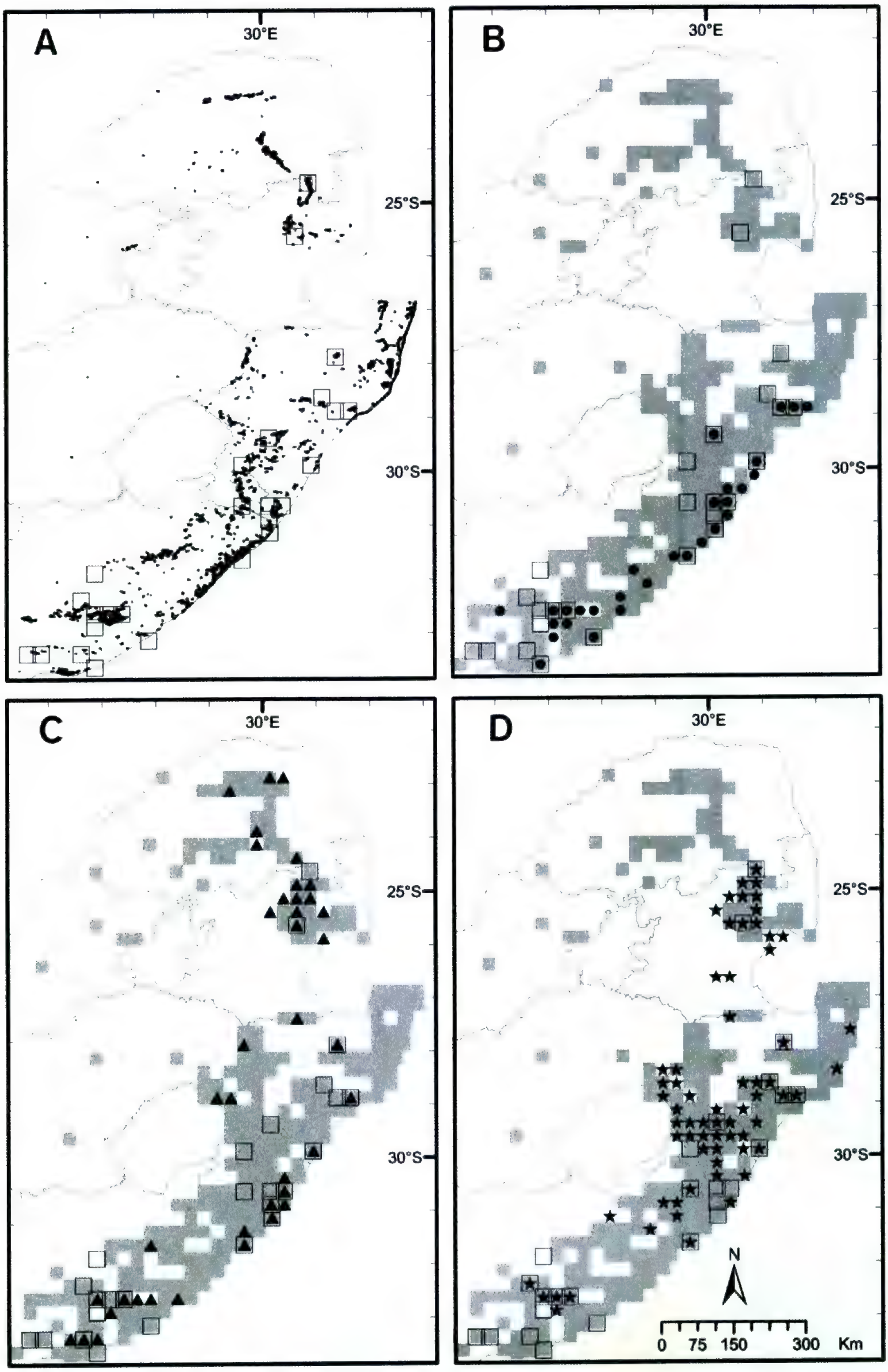

Figure 3. Distribution of forest biome, the fly (*Stenobasipteron wiedemanni*) and members of the *S. wiedemanni* pollination Guild in eastern South Africa. The forest biome is mapped at quarter-degree level for maps B–D (shaded squares). *Stenobasipteron wiedemanni* is shown in each map (□). Plant species are shown on different maps. —A. Actual extent of the forest biome (black spots). —B. *Plectranthus ambiguus* (●). —C. *Brownleea coerulea* (▲). —D. *Impatiens hochstetteri* subsp. *hochstetteri* (★).

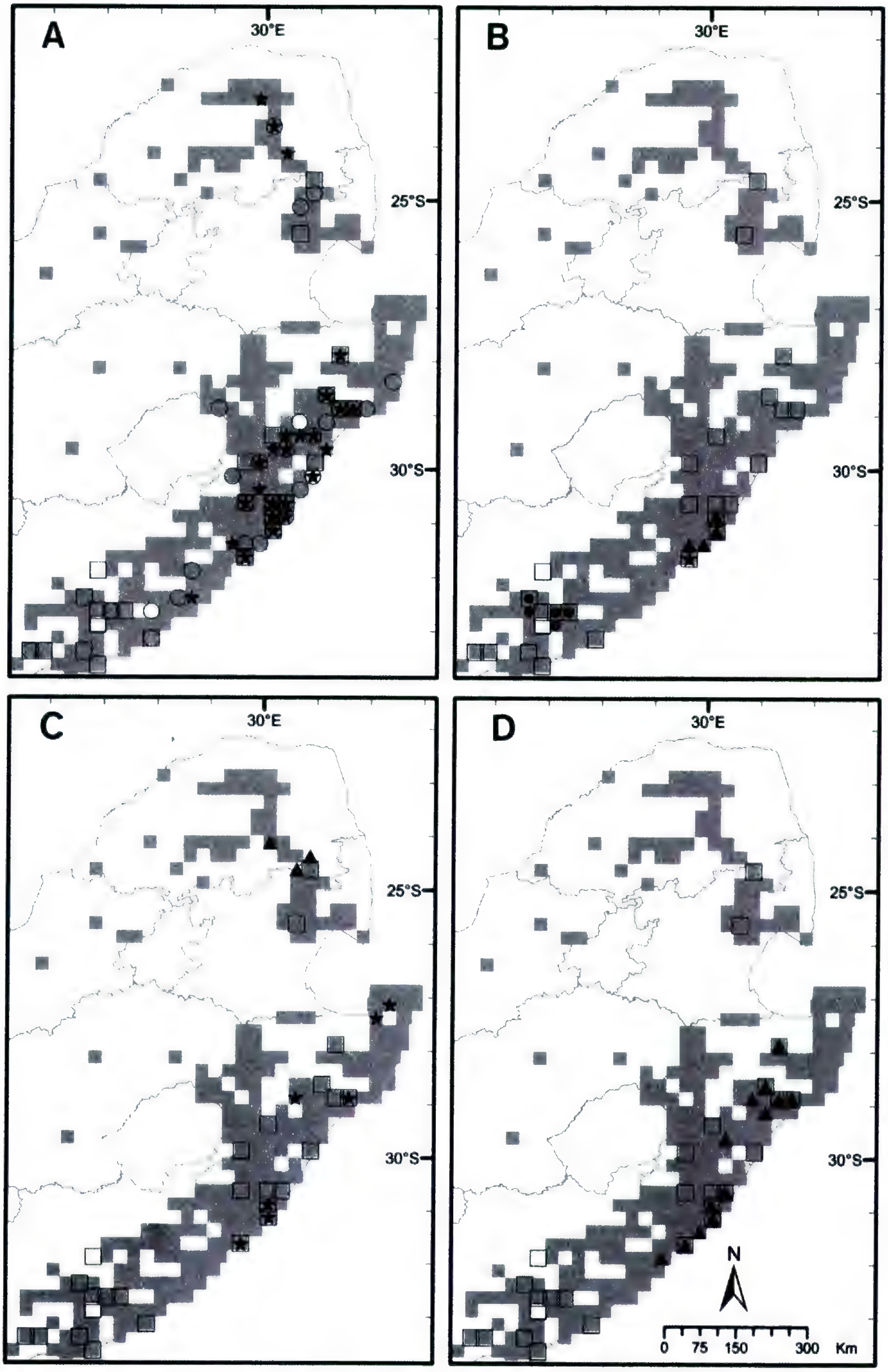

Figure 4. Distribution of forest biome, the fly (*Stenobasipteron wiedemanni*), members and inferred members of the *S. wiedemanni* pollination Guild in eastern South Africa. The forest biome is mapped at quarter-degree level for each map (shaded squares). *Stenobasipteron wiedemanni* is shown in each map (□). Plant species are shown on different maps. —A. *Isoglossa hypoestiflora* (★), *Isoglossa cooperi* (○). —B. *Plectranthus hilliardiae* (▲), *P. reflexus* (★), *Hesperantha huttonii* (●). —C. *Orthosiphon tubiformis* (▲), *P. saccatus*—long-tubed forms (★). —D. *Asystasia varia* (▲).

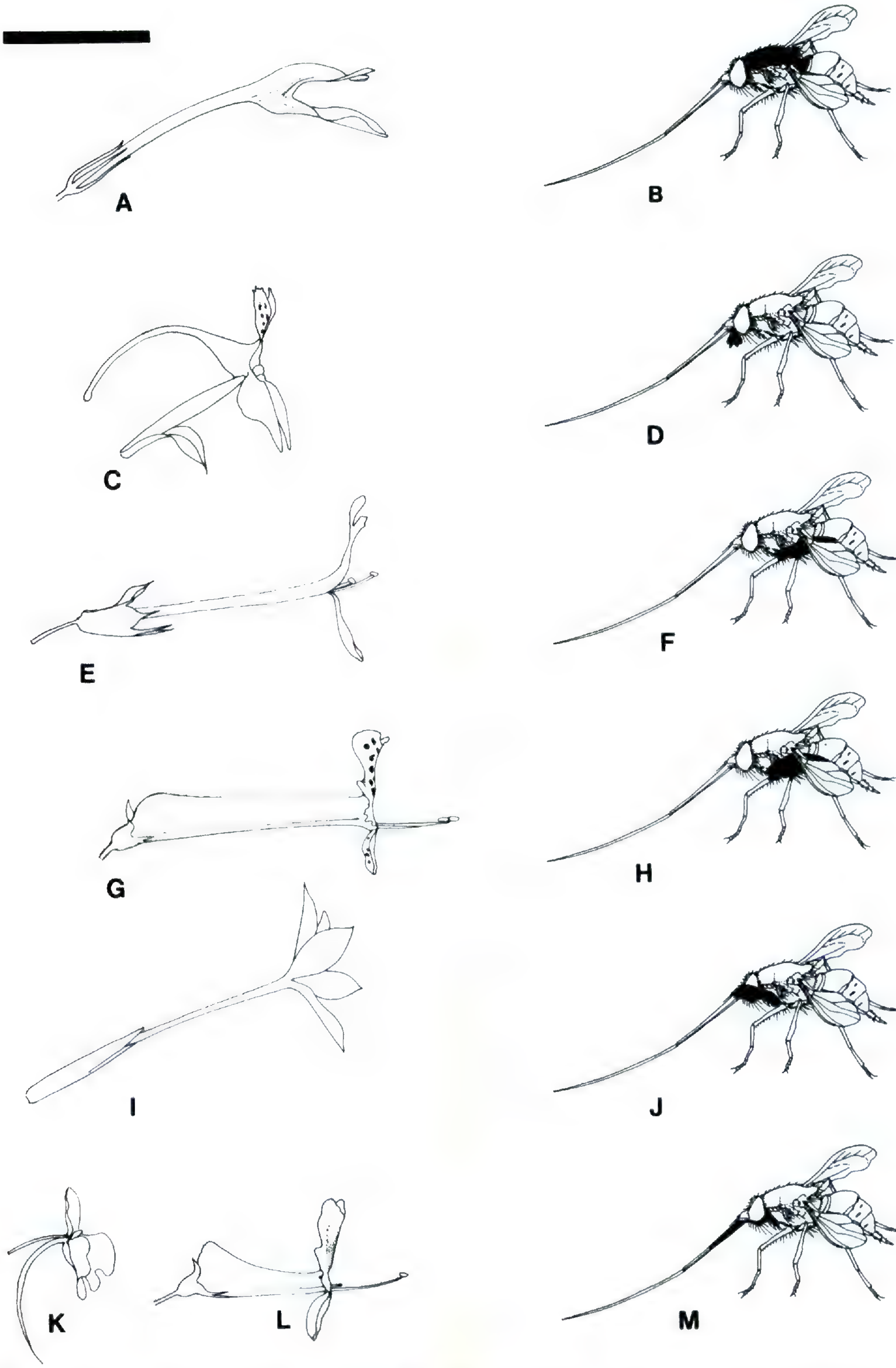

Figure 5. Areas of pollen deposition (indicated by black shading on insect) on *Stenobasipteron wiedemanni* for floral forms in the Guild. —A. *Isoglossa hypoestiflora* (Acanthaceae). —B. Pollen placed dorsally on thorax. —C. *Brownleea coerulea* (Orchidaceae). —D. Pollinaria attached at base of head and proboscis. —E. *Orthosiphon tubiformis* (Lamiaceae). —F. Pollen placed ventrally on thorax. —G. *Plectranthus hilliardiae* (Lamiaceae). —H. Pollen placed ventrally on thorax. —I. *Hesperantha huttonii* (Iridaceae). —J. Pollen placed ventrally and on lower sides of thorax and head. —K. *Impatiens hochstetteri* subsp. *hochstetteri* (Balsaminaceae). —L. *Plectranthus zuluensis* (Lamiaceae). —M. *Impatiens* (K) pollen placed on proboscis; *Plectranthus* (L) pollen placed ventrally on head and thorax. Scale bar 20 mm. Drawn by T. Edwards.

Table 2. Nectar sugars in species belonging to the *Stenobasipteron wiedemanni* pollination guild. G & M = data from Goldblatt and Manning (2000); otherwise data are from the present study. The four *Plectranthus* species with short or medium tubes are indicated by [1].

Species	Nectar		Range of sugars %			Sucrose/ Fru + Glu	Reference
	Volume μl (n)	Conc. %	Fru	Glu	Suc		
Lamiaceae							
Orthosiphon tubiformis	2.7–4.1 (10)	24.5	0–1	0–5	94–100	25.2	G & M
Plectranthus reflexus	0.9–3.2 (8)	—	1	3	96	24.0	
P. hilliardiae	0.2–2.4 (40)	31	5	4	91	10.11	
P. ambiguus	—	—	24	22	54	1.17	
P. saccatus (long tube)	1.4–8.7 (10)	4–18	30	29	41	0.70	
[1]*P. ecklonii*	—	—	9	16	75	3.0	
[1]*P. ciliatus*	0.2–2.8 (25)	29–33	13	15	72	2.57	
[1]*P. fruticosus*	—	24	19	25	56	1.27	
[1]*P. zuluensis*	0.4–1.4 (11)	—	17–19	21–23	57–62	1.5	
Acanthaceae							
Isoglossa hypoestiflora	0.1–5.3 (27)	—	18	33	49	0.96	
Orchidaceae							
Brownleea coerulea	1.3–1.8 (2)	25–27	10	0–11	79–90	5.45	G & M
Iridaceae							
Gladiolus macneilii	4.5–5.8 (5)	26	—	—	—	—	G & M

rich nectar (sucrose:hexose ratio 0.5–0.99), using the categories of Baker and Baker (1990).

Notes on Pollination in Each Family

LAMIACEAE

In *Plectranthus* the deposition of pollen is sternotribic, since the bilabiate flowers have filaments and stamens that are ventrally aligned within the floral tube and lower lip. The long-tubed species force the fly, *Stenobasipteron wiedemanni*, to probe the floral tube fully, which maximizes pollen deposition and subsequent removal from the insect's body. Shorter-tubed species of *Plectranthus* are also visited by the fly, but it is not the only pollinator (Potgieter et al., 1999).

ACANTHACEAE

The flowers of *Isoglossa hypoestiflora* have long, narrow tubes (up to 27 mm, Table 1) that widen to form a raised palate with petal sculpturing on the lower lip, and a hooded upper lip where the anthers and stigma are positioned. Pollen transfer is nototribic on the thorax and abdomen of the fly, with a few grains placed on the proboscis. *Isoglossa cooperi* C. B. Cl. may be conspecific with *I. hypoestiflora*. The species were mapped separately in accordance with current taxonomy (Clarke, 1912).

Hypoestes aristata (Vahl) Sol. ex Roem. & Schult. has a distribution greater than that of the fly (extending into coastal parts of the Western Province and into Tropical Africa), and it is not exclusively pollinated by *Stenobasipteron wiedemanni*; xylocopid bees, tabanid flies, and papilionoid butterflies have been observed as floral visitors (G. Nicholls and G. Upfold, pers. comm.). Insects access nectar from the lilac, bilabiate, medium-tubed flowers (tubes up to 21 mm, Table 1), with filament and style lengths that reach 34 mm (measured at NU) that are crowded into verticillate inflorescences (Balkwill & Getliffe Norris, 1985). *Barleria obtusa* Nees was seen to be visited by *S. wiedemanni* at Oribi Gorge (F. Field, pers. comm.), but bees also visit this species.

ORCHIDACEAE

Brownleea coerulea Harv. ex Lindl. is the only orchid seen to be pollinated by *Stenobasipteron wiedemanni*. We studied it at Stutterheim, where the fly accesses nectar from the slightly recurved spur (20–24 mm long, Table 1) and picks up pollinaria at the base of the proboscis.

BALSAMINACEAE

Impatiens hochstetteri Warb. subsp. *hochstetteri* is a widespread African species ranging from northern Sudan to South Africa. It grows in shaded moist places—often in forests—and flowers throughout the year, with seasonal flowering in some areas

(Grey-Wilson, 1980). Corollas are pink with a curved calyx spur (10–)16–24 mm long (Grey-Wilson, 1980), but specimens from our study areas in KZN (measured at NU) have spur lengths 16–27 mm long. We have seen a number of visits by the fly, but never managed to collect a voucher. One was caught by M. Byrne at Nkandla Forest after observing visits to *I. hochstetteri* subsp. *hochstetteri* (McLellan, pers. comm.), but very little pollen remained on the voucher. *Impatiens* L. pollen adheres dorsally to the proboscis of the fly, since the short spur and sessile anthers prevent deposition elsewhere on the insect's body. The throat of the spur is exceedingly narrow, and the sessile anthers are situated directly above this aperture.

GESNERIACEAE

Streptocarpus formosus (Hilliard & B. L. Burtt) T. J. Edwards is pollinated by *Stenobasipteron wiedemanni* (J. Manning, pers. comm.). Flies enter the flower fully, since the 40–55 mm long corolla (Weigend & Edwards, 1994) is only narrow in the lower part (31–36 mm, Table 1). Pollen deposition is nototribic on the fly thorax. The pale violet corollas have dark stippling in the throat, which acts as a nectar guide, and yellow pigmentation on the floor of the corolla tube. It is a narrow endemic in forest habitats from Umtamvuna to the area just north of Oribi Gorge (NU records), and observations were made at Umtamvuna in January 2002.

IRIDACEAE

Hesperantha huttonii (Baker) Hilliard & Burtt is a day-flowering species with purple flowers and narrow, straight perianth tubes. Flowers have exserted anthers and perianth tube lengths that vary from 22 to 39 mm, which fall into two size classes (Table 1); those with longer tubes occur at the Katberg, but specimens collected outside of the Katberg (in the Amatole Mountains) have shorter tubes (Hilliard & Burtt, 1986), such as the plants studied at Stutterheim in this study (tubes 24–27 mm long). We found *Hesperantha* pollen on *Stenobasipteron wiedemanni* individuals caught in two different years at this site, but we never saw the visits. Our voucher plant specimen of *H. huttonii* had grains of *Plectranthus* pollen on the styles and anthers, which shows that pollinators that visited a nearby *Plectranthus* also visited *H. huttonii.* Subsequent to this observation, P. Goldblatt (pers. comm.) recorded *S. wiedemanni* visiting flowers of *H. huttonii,* confirming our indirect observations.

Discussion

The suite of characteristic floral attributes associated with pollination by *Stenobasipteron wiedemanni* includes long, narrow floral tubes or spurs (Table 1); flower colors in shades of purple, mauve, pale blue, pink, and white; both subtropical and montane forest habitats; and the presence of nectar guides as darker spots or lines in certain species (e.g., *Brownleea coerulea, Hypoestes aristata, Plectranthus hilliardiae* Codd, *P. ecklonii* Benth., *P. zuluensis* T. Cooke, *P. ciliatus* E. Mey. ex Benth., *P. praeternissus* Codd, *P. fruticosus* L'Hér., *P. ambiguus* (Bolus) Codd, *Orthosiphon tubiformis,* and *Streptocarpus formosus*).

Nectar rewards are offered in all studied species and nectar is sucrose dominant or rich. Nectar concentrations are similar to those previously recorded for long-proboscid fly pollinated plants (Goldblatt & Manning, 2000).

Natural forest habitat in southern Africa is largely restricted to the eastern parts of the sub-continent, extending as far west as the eastern section of the Western Cape Province (not fully shown in Figs. 3, 4) (Low & Rebelo, 1996). Observations and museum records show that members of the *Stenobasipteron wiedemanni* Guild are largely limited to forested areas.

In Mpumalanga Province this Guild does not operate in the same kind of closed-canopy, moist forest. *Orthosiphon tubiformis* is visited by *S. wiedemanni* in rocky grassland that appears to have been recently transformed from more wooded to more open vegetation (Goldblatt, pers. comm.), and *Gladiolus macneilii* Oberm. occurs in more wooded savanna or forest margins (Manning et al., 1999). Nevertheless, there is still some tree cover and a similarity in temperature regimes. The KwaZulu-Natal and Eastern Cape forests where *S. wiedemanni* is found are warm coastal or cool mist-belt forests, while the Mpumalanga observations are from cooler, higher altitudes.

At least eight plant species within this pollination Guild appear to rely solely on *Stenobasipteron wiedemanni* for pollination (indicated in Table 1 as having the fly as the only observed visitor to reach nectar). In *Plectranthus reflexus* Van Jaarsv. & T. J. Edwards, an opportunist butterfly visitor was seen (Potgieter & Edwards, 2001), but it is likely that the corolla design is geared toward long-proboscid fly pollination. In *P. ambiguus* visits by two species of long-proboscid bees were seen (Potgieter et al., 1999), but they are unable to reach nectar in most flowers. Some specimens have shorter corolla tubes (20 mm is the lower end of the range, Table 1) and

these may allow exploitation by bees. Other species in the Guild (with shorter corolla tubes) are not solely visited by *S. wiedemanni*, but still need to be included since the fly provides an efficient pollination service (Potgieter et al., 1999).

Discussion by Family

LAMIACEAE

Pollination of *Plectranthus hilliardiae*, *P. reflexus*, *P. ambiguus*, and long-tubed forms of *P. saccatus* has previously been discussed in Potgieter et al. (1999) and Potgieter and Edwards (2001). In most areas where *Stenobasipteron wiedemanni* has been observed, *Plectranthus* species (long- or short-tubed) tend to form a major component of the forest understory. *Orthosiphon tubiformis* occurs in different habitat to forest understory *Plectranthus* species and has been discussed by Goldblatt and Manning (2000).

ACANTHACEAE

Honeybees collect pollen from *Isoglossa hypoestiflora*, but the long, narrow corolla tube prohibits nectar access. Honeybees would not contribute to significant pollen carryover over large distances, since pollen is groomed into the scopae before the worker bees return to their hives. *Isoglossa cooperi* closely resembles *I. hypoestiflora* in floral shape and size, differing only in the presence of glandular hairs on the calyx and bracts. The species are often sympatric (Fig. 4A). From a pollination perspective, these two species are very similar and fit the *Stenobasipteron wiedemanni* pollination Guild. They occur in afromontane and scarp forest and are generically anomalous with respect to flower color and corolla morphology. Most *Isoglossa* Oerst. species in South Africa are hymenophilous (pers. obs.), with creamy white flowers and short corolla tubes (mostly less than 10 mm in length). These creamy white species are common in savanna and tropical and subtropical forests.

The observation of visits to *Hypoestes aristata* shows that *Stenobasipteron wiedemanni* may form part of a more generalized suite of pollinators in species with shorter floral tubes. As in shorter-tubed *Plectranthus* species, the fly still contributes to pollen carryover, since the elongate anther filaments deposit pollen on the body of the fly and the elongate style is able to remove pollen from this position. A similar situation exists in *Barleria obtusa*, where long-proboscid bees can also access nectar by crawling into the widened distal part of the corolla tube.

ORCHIDACEAE

The record for long-proboscid fly pollination in *Brownleea* Harv. ex Lindl. (Goldblatt & Manning, 2000) highlights the disjunction between grassland- and forest-growing species. *Brownleea macroceras* Sond. is pollinated by *Prosoeca ganglbaueri* (Johnson & Steiner, 1995), which occurs in montane grassland at high altitudes. By contrast, *B. coerulea* is a forest margin species of lower altitudes and is pollinated by *Stenobasipteron wiedemanni*. *Brownleea coerulea* is a widespread species (Fig. 3C) that also occurs in Madagascar, where its pollination has not been studied.

BALSAMINACEAE

The floral visits by *Stenobasipteron wiedemanni* to *Impatiens hochstetteri* subsp. *hochstetteri* are the first published records of nemestrinid fly pollination in the Balsaminaceae. This plant species is widespread across Africa, but the distribution of *S. wiedemanni* elsewhere in Africa is not known. Grey-Wilson (1980) recorded butterflies as pollinators of the "flat type" flowers in the section to which *I. hochstetteri* subsp. *hochstetteri* belongs, yet little information is available on the pollination of specific *Impatiens* L. (Grey-Wilson, 1980). We have observed papilionoid butterfly visits to *I. hochstetteri* subsp. *hochstetteri* at Ferncliffe Nature Reserve in Pietermaritzburg (KZN) confirming the above. The distribution of *Impatiens hochstetteri* subsp. *hochstetteri* in southern Africa (Fig. 3D) shows a number of plots outside forested areas. This species relies on moist forest habitats and may occur in scrub forest patches that are below the resolution of our Geographic Information System that was used for mapping.

GESNERIACEAE

Very little is known about pollination in *Streptocarpus* (Hilliard & Burtt, 1971), and it is likely that *Stenobasipteron wiedemanni* is the pollinator of a number of *Streptocarpus* species that conform to the floral morphology of *S. formosus*.

IRIDACEAE

The genus *Hesperantha* comprises many scented, pale species with crepuscular anthesis that are thought to be pollinated by moths (Goldblatt, 1984). Contrary to this pattern, *H. huttonii* is odorless, has diurnal anthesis and colored flowers—attributes suited to nemestrinid fly pollination. Long-proboscid fly pollination of day-flowering species of *Hesperantha* is not uncommon. *Hesperantha latifolia*

(Klatt) M. P. de Vos is pollinated by *Prosoeca peringueyi* in Namaqualand, while *H. grandiflora* G. J. Lewis, *H. scopulosa* Hilliard & B. L. Burtt, and *Hesperantha* cf. *woodii* Baker are pollinated by *P. ganglbaueri* in grasslands in the eastern parts of the country (Goldblatt & Manning, 2000). In Mpumalanga *Hesperantha brevicaulis* (Baker) G. J. Lewis is pollinated by *Stenobasipteron wiedemanni* (Goldblatt & Manning, 2000). The switch between moth and nemestrinid pollination was recently also recorded in *Zaluzianskya* F. W. Schmidt (Scrophulariaceae) by Johnson et al. (2002).

Inferred Members of the *Stenobasipteron wiedemanni* Guild

There are a number of other plant species that may belong to the *Stenobasipteron wiedemanni* pollination Guild. Labiate species such as *Stachys tubulosa* MacOwan, *Salvia repens* Burch. ex Benth. var. *keiensis* Hedge, *Salvia scabra* L.f., and *Hemizygia ramosa* Codd have been suggested as candidates (Potgieter & Edwards, 2001).

Manning et al. (1999) suggested that *Gladiolus sekukuniensis* P. Winter and *G. saxatalis* Goldblatt & J. C. Manning (both Iridaceae) are pollinated by *Stenobasipteron wiedemanni* in the highlands of Mpumalanga and Northern (Limpopo) Province, since they have similar morphology and phenology to *G. macneilii* and occur in forest margins and wooded savannas.

Streptocarpus species (Gesneriaceae) that may conform to this Guild include *S. rexii* (Bowie ex Hook.) Lindl. (forests of the Western and Eastern Cape Provinces, from Knysna to Kokstad), *S. primulifolius* Gand. (forests of the Eastern Cape Province and KwaZulu-Natal), and *S. cyaneus* S. Moore (forests of Mpumalanga Province).

Pelargonium transvaalensis (Geraniaceae) is a forest species of the eastern seaboard. It is likely that *Stenobasipteron wiedemanni* is the pollinator, since the hypanthial tubes are ca. 20 mm long and pink in color.

Rhinacanthus gracilis Klotzsch and *Asystasia varia* N. E. Br. (both Acanthaceae) are also likely to belong to this Guild; *R. gracilis* was inferred as a member of the *Prosoeca ganglbaueri* pollination system of Goldblatt and Manning (2000) that included *Stenobasipteron wiedemanni*. *Rhinacanthus gracilis* is a subtropical species of forest and woodland; it has mauve to white narrow floral tubes ca. 20 mm long. Similarly, *A. varia* has mauve flowers with tubes 35–40 mm long of which the basal half to two-thirds is narrowed, and the lower floral lobe has a raised palate with violet nectar guides (Edwards, 1988). It occurs in forest patches ranging from northern KwaZulu-Natal to the Eastern Cape, a distribution coinciding with that of *Stenobasipteron wiedemanni* (Fig. 4D). *Asystasia gangetica* T. Anderson and *A. pinguifolia* T. J. Edwards are bee-pollinated species of grasslands (Edwards, 1988) with shorter tubes and white flowers.

Asystasia varia may indicate a shift from bee to long-proboscid fly pollination associated with elongation of the floral tube and a flower color shift from creamy white to mauve. A similar shift may have happened in *Isoglossa* (also Acanthaceae), where most species have creamy white flowers with short corolla tubes (adapted to bee pollination), but *I. hypoestiflora* and *I. cooperi* have mauve flowers with longer tubes. Without cladistic analyses we can only speculate about such shifts. In the Iridaceae it has been shown that long-proboscid fly flowers are often closely related to ancestors pollinated by long-tongued bees (Goldblatt & Manning, 2000).

Conclusions

The *Stenobasipteron wiedemanni* pollination Guild should be recognized separately from the three Guilds suggested by Goldblatt and Manning (2000). There is no overlap in the plant species pollinated by this fly compared to the other three Guilds. On the basis of habitat there is no or very little overlap in the distribution of the fly species. Unlike the mostly pink flowers with dark pink to red markings pollinated by the *Prosoeca ganglbaueri* Guild (sensu Goldblatt & Manning, 2000), the *S. wiedemanni* Guild consists of flowers with shades of purple, mauve, pale blue, pink, and white. In cases where flower color is similar, e.g., the blue-flowered *Nivenia stenosiphon* Goldblatt and pale pink-flowered *Nerine* Herb. and *Brunsvigia* Heist. species that were included in the *Prosoeca ganglbaueri* Guild of Goldblatt and Manning (2000), there is no overlap in plant species at the microgeographic scale. The *S. wiedemanni* pollination Guild is thus limited by the (forest) distribution of the fly, rather than by floral color or shape.

We have confirmed the existence of long-proboscid fly pollination in the Acanthaceae, as suggested by Goldblatt and Manning (2000) and report it here for the first time in the families Balsaminaceae and Gesneriaceae.

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Appendix 1. Vouchers of *Stenobasipteron wiedemanni* (Diptera, Nemestrinidae) lodged at Natal Museum, Pietermaritzburg. KZN = KwaZulu-Natal Province, E Cape = Eastern Cape Province.

Collector's no.	Locality (all in South Africa)	Plant	Date
C. Potgieter 1	KZN: Umtamvuna	*Plectranthus ambiguus*	17 Mar. 1995
C. Potgieter 2	KZN: Umtamvuna	*P. ambiguus*	18 Mar. 1996
C. Potgieter 3	KZN: Umtamvuna	*P. ambiguus*	15 Mar. 1996
C. Potgieter 102	KZN: Oribi Gorge	*P. ciliatus*	25 Mar. 1997
C. Potgieter 103	KZN: Oribi Gorge	*P. zuluensis*	25 Mar. 1997
C. Potgieter 154	KZN: Karkloof, Leopards Bush	*P. fruticosus*	3 Mar. 1999
C. Potgieter 155	KZN: Karkloof, Leopards Bush	in spider web	3 Mar. 1999
C. Potgieter 170	KZN: Ongoye Forest	on ground (with *I. hypoestiflora* pollen)	22 Apr. 1999
C. Potgieter 191	E Cape: Port St Johns	*P. praetermissus*	9 Mar. 1998
C. Potgieter 192	E Cape: Stutterheim, Kologha Forest	*P. ciliatus*	5 Mar. 1998
C. Potgieter 193	E Cape: Stutterheim, Kologha Forest	*P. ciliatus*	5 Mar. 1998
C. Potgieter 194	E Cape: Stutterheim, Kologha Forest	*P. ecklonii*	5 Mar. 1998
C. Potgieter 195	E Cape: Stutterheim, Kologha Forest	*P. ecklonii*	5 Mar. 1998
C. Potgieter 197	E Cape: Stutterheim, Kologha Forest	*P. ecklonii*	29 Feb. 2000
C. Potgieter 198	E Cape: Stutterheim, Kologha Forest	*Brownleea coerulea*	29 Feb. 2000
F. Field s.n.	KZN: Oribi Gorge	*Barleria obtusa*	5 Apr. 1997
M. Byrne s.n.	KZN: Nkandla Forest	*Impatiens hochstetteri*	31 Jan. 2001

Appendix 2. Vouchers for studied plant species lodged at NU Herbarium, Pietermaritzburg. References for pollinator observations and/or floral tube measurements are given where this has been recorded in addition to observations in the current study. P & E = Potgieter & Edwards, P et al. = Potgieter et al., G & M = Goldblatt & Manning, G-W = Grey-Wilson, W & E = Weigend & Edwards. KZN = KwaZulu-Natal Province, E Cape = Eastern Cape Province, PMB = Pietermaritzburg.

Plant species (arranged by family)	Collector's no.	Locality (all in South Africa)	Reference of previous work
Lamiaceae			
Plectranthus ambiguus (Bolus) Codd	*C. Potgieter 86*	KZN: Umtamvuna	P & E (2001)
P. hilliardiae Codd	*C. Potgieter 110, 111, 112*	KZN: Umtamvuna	P & E (2001)
P. reflexus Van Jaarsv. & T. J. Edwards	*T. Edwards 1554*	E Cape: Port St Johns	P & E (2001)
P. saccatus Benth. (long-tubed)	*C. Potgieter 107, 120*	KZN: Umtamvuna	P & E (2001)
P. ecklonii Benth.	*C. Potgieter 65, 114*	KZN: Oribi Gorge	P et al. (1999)
	C. Potgieter 70	KZN: Umtamvuna	
P. praetermissus Codd	*T. Edwards 1556*	E Cape: Port St Johns	
P. zuluensis T. Cooke	*C. Potgieter 64, 118*	KZN: Oribi Gorge	P et al. (1999)
P. ciliatus E. Mey. ex Benth.	*C. Potgieter 67*	KZN: Oribi Gorge	P et al. (1999)
	C. Potgieter 68, 69, 116	KZN: Umtamvuna	
	C. Potgieter 136	KZN: PMB, Horncliffe	
P. fruticosus L'Hér.	*C. Potgieter 66*	KZN: Oribi Gorge	
	C. Potgieter 134	KZN: PMB, Horncliffe	
	C. Potgieter 144	KZN: Karkloof, Leopards Bush	
Orthosiphon tubiformis R. D. Good			G & M (2000); P & E (2001)
Acanthaceae			
Isoglossa hypoestiflora Lindau	*C. Potgieter s.n.*	KZN: Oribi Gorge	G. Nicholls (pers. comm.)
	C. Potgieter & D. Thompson 735	KZN: Creighton, Hlabeni Forest	
Hypoestes aristata (Vahl) Sol. ex Roem. & Schult.			G. Nicholls (pers. comm.)
Barleria obtusa Nees			F. Field (pers. comm.)
Orchidaceae			
Brownleea coerulea Harv. ex Lindl.	*Edwards & Potgieter 1841*	E Cape: Stutterheim, Kologha Forest	G & M (2000)
Balsaminaceae			
Impatiens hochstetteri Warb. subsp. *hochstetteri*	*C. Potgieter & D. Thompson 744*	KZN: Creighton, Hlabeni Forest	McLellan (pers. comm.); G-W (1980)
Gesneriaceae			
Streptocarpus formosus (Hilliard & B. L. Burtt) T. J. Edwards			W & E (1994); Manning (pers. comm.)
Iridaceae			
Hesperantha brevicaulis (Baker) G. J. Lewis			G & M (2000)
H. huttonii (Baker) Hilliard & B. L. Burtt	*Edwards & Potgieter 1841a*	E Cape: Stutterheim, Kologha Forest	Goldblatt (pers. comm.)
Gladiolus macneilii Oberm.			G & M (1999)

THE FLORAL BIOLOGY OF *MELASPHAERULA* (IRIDACEAE: CROCOIDEAE): IS THIS MONOTYPIC GENUS POLLINATED BY MARCH FLIES (DIPTERA: BIBIONIDAE)?[1]

Peter Goldblatt,[2] *John C. Manning,*[3] *and Peter Bernhardt*[4]

Abstract

Bibio longirostris, a small (ca. 5 mm long) nectar-feeding fly (proboscis ca. 1 mm long) was found to be the only visitor to the small, zygomorphic flowers (8–10 mm long) of *Melasphaerula ramosa*, a species endemic to the southern African winter-rainfall zone. Each captured fly carried the pollen of *M. ramosa* exclusively, with grains deposited on the dorsal part of the thorax. Observations showed that these insects contacted both dehisced anthers and stigmatic surfaces of style branches while evidently foraging on nectar secreted from septal nectaries into the base of the floral tube. Experimental hand pollinations showed that *M. ramosa* is self-compatible, and some flowers undergo mechanical self-pollination (autogamy) in the absence of insect visitors. Pollination of this genus of Iridaceae by bibionids represents a new syndrome within the broad category of fly pollination and expands the range of pollination mechanisms reported in this family. As there is comparatively little scientific literature confirming bibionid pollination throughout the world, we compare the floral biology of *M. ramosa* with available litrerature on pollination by other microdipterans in the Araceae, Hydrophyllaceae, Saxifragaceae, Orchidaceae, and Sterculiaceae.

Key words: Bibionidae, Iridaceae, microdipteran flies, pollination biology, southern Africa.

As in most families of animal-pollinated plants, studies of the pollination biology of the African Iridaceae have shown that species of most genera (e.g., *Chasmanthe* N. E. Br., *Gladiolus* L., *Hesperantha* Ker Gawl., *Ixia* L., *Lapeirousia* Pourret, *Moraea* L., *Nivenia* Vent., and *Sparaxis* Ker Gawl.) have large, brightly colored flowers that are pollinated by a range of relatively large-bodied insects (> 8 mm long) or nectarivorous passerine birds. Insect pollinators include bees representing five families (Andrenidae, Apidae, including anthophorines, Colletidae, Halictidae, and Melittidae), hopliine or "monkey" beetles (Scarabaeidae), Lepidoptera including diurnal butterflies and crepuscular moths, and various Diptera. In particular, fly pollination in the Iridaceae of southern Africa is unusually complex and extensive. Just as guilds of pollinators often represent specialized, sometimes closely related animals, so the flowers produced by individual species of the Iridaceae of southern Africa often reflect suites of predictable modes of floral presentation, attractants, and edible rewards (Bernhardt & Goldblatt, 2000).

In particular, fly pollination, first documented in the Iridaceae of southern Africa by Vogel (1954), breaks down into at least three syndromes based on a combination of proboscis length, color recognition, and scent perception. The first syndrome, involving pollination by short-tongued carrion and dung flies (Muscidae, Scathophagidae) of flowers of the genus *Ferraria* Burm. and some *Moraea* spp. (Vogel, 1954; Goldblatt & Bernhardt, 1999), represents the classic characters of dull-colored and often blotched or speckled pigmentation and foul odors that Faegri and van der Pijl (1979) referred to as *sapromyophily*. In the second syndrome, involving the character suites of mainly unscented flowers in the genera *Geissorhiza* Ker Gawl., *Ixia*, *Lapeirousia*, and *Sparaxis*, pollination is by flies with medium-length mouthparts in the families Acroceridae, Bombyliidae, and short-proboscid Tabanidae. It represents a more generalist

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[2] B. A. Krukoff Curator of African Botany, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A. peter.goldblatt@mobot.org.

[3] Compton Herbarium, National Botanical Institute, P. Bag. X7, Claremont 7735, South Africa.

[4] Department of Biology, St. Louis University, St. Louis, Missouri 63103, U.S.A.

Table 1. Voucher data for plant and insect species studied.

South Africa. Western Cape: near Moorreesburg, 24 Aug. 2000
Melasphaerula ramosa: *Goldblatt 11425* (MO, NBG)
Bibio longirostris: *Goldblatt s.n.*, Oregon State University; KwaZulu-Natal Museum, South Africa

syndrome in which the flowers are also pollinated by bees, butterflies, noctuid moths, and/or hopliine beetles. The third syndrome involves those large-bodied species of the fly families Nemestrinidae and Tabanidae that have evolved elongated probosces two to three times the length of their bodies, 15–24 mm long (Goldblatt & Manning, 2000), and pollinate flowers of several species in the genera *Babiana, Geissorhiza, Gladiolus, Hesperantha, Lapeirousia,* and *Nivenia.* Individual plant species with this specialized system are pollinated exclusively by only one to three species of these long-proboscid flies. Their flowers, which have the longest floral tubes in the family, also exhibit predictable and stereotyped patterns of pigmentation (Goldblatt et al., 1995; Manning & Goldblatt, 1996, 1997; Goldblatt & Manning, 1999, Goldblatt et al., 2000a, b).

Dipteran foragers to flowers of species of southern African Iridaceae with small, relatively inconspicuous flowers have, however, long eluded us. Populations of *Melasphaerula ramosa* (Burm. f.) N. E. Br., the only species in this monotypic genus of the southern African winter-rainfall zone, were examined at several sites for pollinator activity for five years without results until the spring of 2000, when we finally encountered a population of *Melasphaerula* Ker Gawl. in which insect activity was evident and unambiguous. We report the results of these observations, which represent a novel mode of fly pollination for the Iridaceae.

Materials and Methods

A small population comprising some 45 plants of *Melasphaerula ramosa* near Moorreesburg, Western Cape, South Africa (voucher *Goldblatt 11425*, 24 Aug. 2000 (MO, NBG); Table 1), yielded abundant insect visitors. This was the first time insect activity had been observed in the species, despite attempts at several other sites (totaling about 20 hours) to record and identify pollinators of this plant. *Melasphaerula* plants were also examined in the field for attractants and rewards as outlined elsewhere (Goldblatt et al., 1995, 2000a, b; Goldblatt & Manning, 1999).

Insects seen to visit flowers in such a way as to contact either the anthers or stigmas (which are partly concealed from view by the visiting insect's body) were captured and killed using ethyl acetate fumes. Captured insects were examined for presence of pollen. Visible pollen samples were removed using a dissecting needle and mounted on slides in Calberla's fluid and examined under the compound microscope.

Compatibility relationships of *Melasphaerula* were examined in a greenhouse (Portland, Oregon) using two plants of a single genet. Plants were isolated from insect foragers with nylon netting. Individual flower buds were tagged with jeweller's tags. For plant 1: when the perianth lobes expanded and the style branches unfolded, then assumed to be receptive, we self-pollinated the flower by hand with the contents of dehiscent anthers from the same flower (autogamy) or flowers on the same inflorescence (geitonogamy). The pollinated flowers were then checked after 21 days (three weeks) to observe capsule production. For plant 2: to determine whether mechanical self-pollination (autogamy) occurs in flowers in the absence of pollen vectors, the plant was kept isolated from insect foragers, but was not hand manipulated in any way.

Voucher specimens of *Melasphaerula* are housed at the herbaria at Kirstenbosch National Botanical Garden, Cape Town (NBG), and the Missouri Botanical Garden, St. Louis (MO). Captured insect visitors, identified as *Bibio longirostris* MacQuart by Scott Fitzgerald, Oregon State University, Corvallis, and voucher specimens are housed there and at the KwaZulu-Natal Museum, Pietermaritzburg, South Africa (Table 1).

Results

The distribution of *Melasphaerula ramosa* extends along the coast and near interior of southern Africa from southwestern Namibia south and east to the Baviannaskloof, Eastern Cape, South Africa. Plants show a preference for shady habitats, often growing under shrubs, small trees, or in the shelter of rocks, usually favoring cool, southerly slopes that remain moist during the winter and spring months, June to September. Flowering occurs from early August to October. The flowers are borne on a branched and often highly ramified, panicle-like inflorescence, 20–80 cm high. The lax, somewhat drooping branchlets are spikes, each bearing 3 to 6 half-nodding flowers that open sequentially and acropetally. Despite the small size of the flowers (8–10 mm long), the number of branchlets ensures that

each plant bears several to many flowers open at any time during the flowering season.

Individual flowers last two to three days, remaining open once the tepals expand by early to mid morning of the first day of anthesis. The zygomorphic, bilaterally symmetric flowers are cream to dull yellow with the lower three tepals bearing a purple to maroon median streak (Fig. 1A, B). The tepals, 6–9 × 2–3 mm, are directed forward, forming a gullet-like cup, and taper to attenuate tips. The tepals are united basally into a short tube, less than 1 mm long (Fig. 1C), at the apex of which the filaments are inserted. The filaments are unilateral, lie parallel to one another, and arch upward below

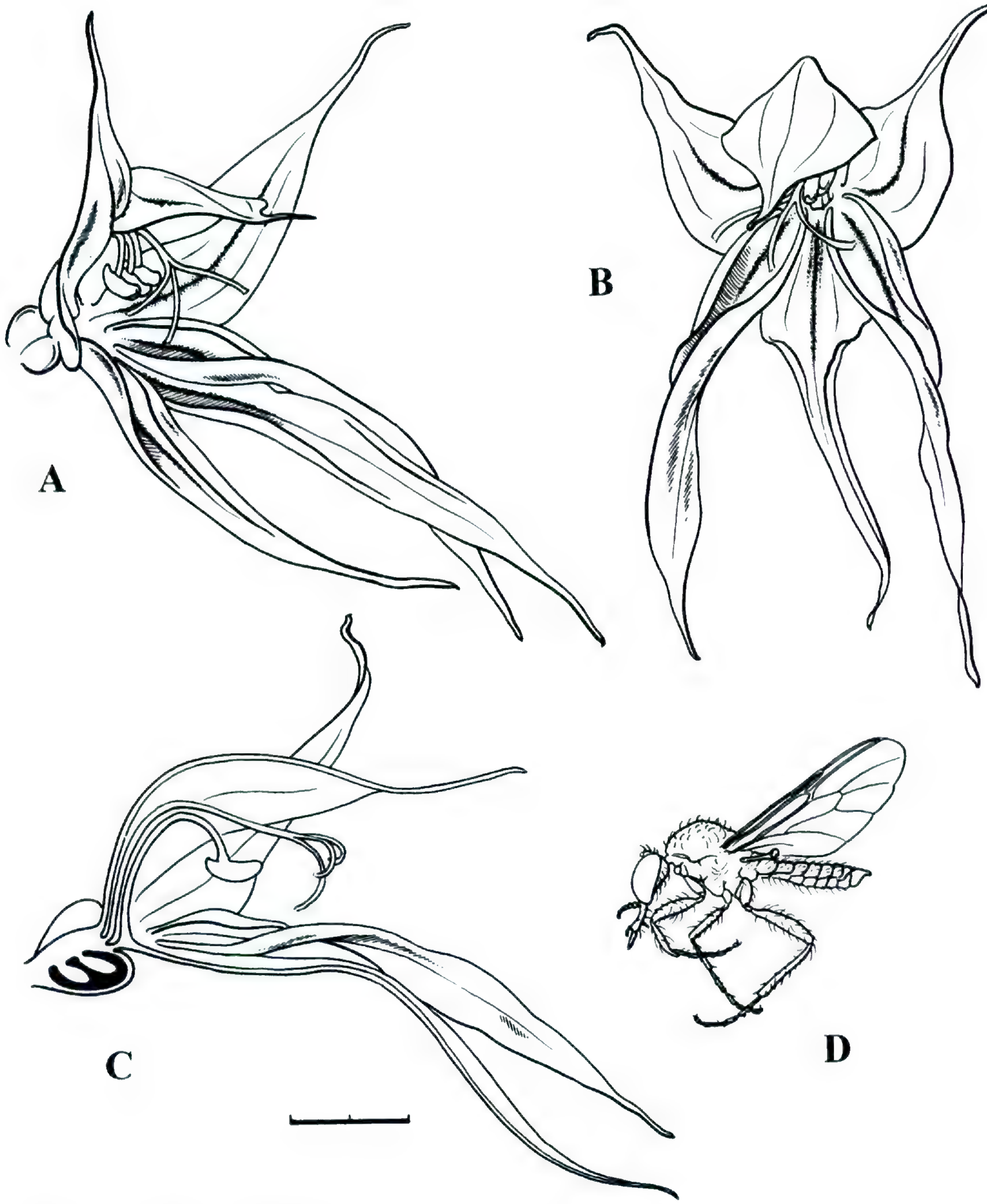

Figure 1. Flowers of *Melasphaerula ramosa* (*Goldblatt 11425*, MO, NBG) and the bibionid fly, *Bibio longirostris* (vouchered by specimens at Oregon State University). —A, B. Lateral and frontal view of the flower. —C. Longitudinal section of flower. —D. Male *Bibio longirostris*. Scale bar = 2 mm.

the hooded dorsal tepal, which much exceeds the stamens. Each filament bears a short, oblong, loculicidally dehiscent anther ca. 1 mm long. The three anthers lie parallel to one another and face downward, toward the extended lower tepals. The filiform style arches upward, posterior to the stamens, arching over them and dividing 1–2 mm beyond the anthers into three filiform, recurved branches (Fig. 1A–C). Physical contact between the pollen contained in the anthers and the stigmatic surfaces of the style branches is prevented by the spatial distance of 1–2 mm between these organs. We infer that self-pollination does not occur in open flowers (but see below). A pollinating insect must climb into the flower and push its proboscis into the floral tube in order to contact either the anthers or the style branches, which are hidden from lateral view by the weakly divergent tepals. When the flowers wilt and the tepals close, stigma lobes and pollen-bearing anthers sometimes come into contact with one another.

Flowers are protandrous. On the morning that the tepals unfold, anthers are dehiscent but the style branches remain clasped together. Later during the afternoon of the same day the style branches, which have adaxial stigmatic surfaces, expand, then separate from one another and recurve. As flowers wilt and the tepals collapse the recurved tips of the style branches will sometimes contact anthers and selfing can occur at this time.

Flowers of some populations have a distinctive, musty-foetid odor that is commonly associated with small, cream or pale yellow flowers, as, for example, in southern African species of *Rhus* L. (Anacardiaceae), while in others no scent can be detected by the human nose. We were unable to measure or detect the presence of nectar by the taste test (brushing the excised base of the floral tube against the tongue), but transverse sections of the ovary showed the presence of septal nectaries of the type found in nearly all members of Iridaceae subfamily Crocoideae (Goldblatt, 1990; Goldblatt & Manning, 1999; Rudall et al., 2003). We therefore assume the presence of trace amounts of nectar.

Populations of *Melasphaerula ramosa* were observed at several sites in southern Africa over the past five years without result, but abundant insect activity was detected over a period of 4 hours on two separate days at one study site in August 2000. These flowers were visited exclusively by small, black-bodied flies, later identified as *Bibio longirostris* (Bibionidae) (Fig. 1D). These insects were seen flying from one inflorescence to another, entering individual flowers and visiting other flowers of *Melasphaerula*. Curiously, all 10 individuals collected (Table 1) were males (B. Stuckenberg, pers. comm.).

The fly, *Bibio longirostris*, typically crawled over the outside of the *Melasphaerula ramosa* flower before climbing into the gullet-like perianth. The narrow perianth severely restricts the movement of the insect as it moves forward, presumably foraging on nectar. Its movement results in its dorsal thorax contacting pollen lying in the dehisced anthers or the stigmatic surfaces of the style branches. Visits lasted from 25 seconds to over one minute. These flies have a body length of 4.5–5.0 mm (measured from the base of the proboscis to the tip of the abdomen) ($n = 10$) and a narrow proboscis approximately 0.8–1.0 mm in length ($n = 10$) that individuals presumably used to probe into the floral tube. Flies did not scrape the anthers for pollen. Contacts between flies and anthers remained passive. A fly exited the flower by crawling in reverse and was observed to either leave the site or visit another flower on the same or another inflorescence. Flowers in the female phase have the stigmatic style branches slightly forward of and below the anthers (Fig. 1C) when fully extended and thus cannot avoid contact with the dorsal part of a fly's body when it attempts to forage on nectar. *Bibio longirostris* was not seen visiting any other flowers at our study site.

Each captured fly carried a visible load of yellow pollen on the dorsal portion of its thorax. Compound microscopy of pollen removed from fly thoraxes showed features identical to the boat-shaped grains taken from anthers of *Melasphaerula ramosa*, i.e., the grains have a perforate, micropunctate exine and a prominent, two-banded operculum lying across the surface of the aperture (Goldblatt et al., 1991). Pollen of no other plant species was found in our microscopic preparations.

Fruit set in our study population of *Melasphaerula ramosa* was not particularly high: randomly selected plants ($n = 5$) in the population of ca. 45 plants showed 40%–60% of flowers on the same inflorescence producing capsules. Although each of the three locules in the unfertilized ovary contain two or three pairs of ovules, capsules contained between 5 and 12 seeds, with a maximum of 4 seeds in any one of the three locules in the same ovary.

Self-compatibility studies showed that of the 10 flowers self-pollinated by hand a total of 9 developed into capsules. The Mean number of seeds per capsule in hand-pollinated flowers was 5. However, in the flowers of the second plant isolated from both insect and hand-pollination 25%–80% of the total flowers on an inflorescence branch set capsules via mechanical autogamy. Flowers that self-pollinated

spontaneously in the greenhouse contained between 1 and 13 fully developed seeds. Thus, *Melasphaerula ramosa*, at least in our study population, is self-compatible and shows a variable mechanical autogamy in the absence of native pollinators.

Discussion

Flies of the family Bibionidae (March flies), including the genus *Bibio* Geoffroy, are described as small- to medium-sized black flies with short or occasionally elongate probosces, that feed predominantly on nectar as winged adults (Skartveit, 1997; Gilbert & Jarvis, 1998), while larvae are terrestrial saprophages, or possibly herbivores (Barraclough & Londt, 1985). Visits to flowers by bibionids have, however, rarely been reported in the African flora, although bibionid species in the genus *Dilophus* Meigen are often collected on flowers in southern Africa, presumably while feeding on nectar. Johnson and Steiner (1994) showed that *Disa obtusa* (Orchidaceae), a species of the southwestern Cape, South Africa, is pollinated by *Bibio turneri* Edwards. These flies carried pollinaria attached to their ventral body surface just posterior to the head. Flies moved from one flower to another on the inflorescences of this orchid, which does not offer nectar but has a strong, musty scent. The reward in *Melasphaerula* flowers is equally puzzling, for nectar is difficult to detect but, like *Disa obtusa* Lindl., the flowers often produce a distinctive, often strong musty odor. The flowers of *D. obtusa* are similar in size and coloring to those of *Melasphaerula* and also have dark maroon streaks on the tepals.

The observations of pollination by bibionid flies in *Melasphaerula* increases the range of insect families known to pollinate members of the Iridaceae, both in southern Africa and across the family's near pandemic distribution. In addition, the apparent dependence of *M. ramosa* on a single genus of flies (*Bibio*) in the Bibionidae now expands the three known modes of fly-pollination in the southern African Iridaceae to four separate syndromes of floral presentation. The distinctive form and small size of *M. ramosa* flowers with their hooded dorsal tepal and attenuate lower tepals, coupled with their distinctive odor and pigmentation pattern, is so atypical that they appear unique among the Iridaceae, and apart from *Disa obtusa* we know of no other plants with similar flowers in southern Africa. Thus, few, if any, additional examples of bibionid pollination exploiting this type of floral presentation are expected in the Iridaceae or any other family.

In contrast to bibionid pollinators, the tabanid and nemestrinid flies with large bodies and ultra-long probosces are far more common and important as primary agents of pollen dispersal for the species-rich genera of Iridaceae in southern Africa (e.g., *Babiana*, *Geissorhiza*, *Gladiolus*, and *Hesperantha*). These flies also pollinate one to several species in various smaller genera (e.g., *Lapeirousia*, *Nivenia*, *Sparaxis*, and *Tritonia*; Goldblatt & Manning, 2000).

What is unique about the role of bibionids in the pollination of *Melasphaerula ramosa* is that they appear to be the only pollinators of these tiny but complex flowers. While flies with small bodies and short mouthparts contribute to the pollination of many Iridaceae in southern Africa, they usually comprise part of a diverse spectrum of pollen vectors. These generalist flowers are usually pollinated by a mix of insects belonging to different orders in which flies with shorter mouthparts and smaller bodies disperse pollen in concert with hopliine beetles and/or anthophorine bees or tabanids (Goldblatt et al., 1998a, 2000a; Goldblatt & Bernhardt, 1999). These generalist systems incorporating small flies with other insect pollinators are associated with radially symmetrical, salver- or bowl-shaped flowers with bright, contrasting pigmentation very different from the narrow, zygomorphic or bilaterally symmetric perianth, and dull coloration of *M. ramosa* (Goldblatt et al., 1998b).

There is comparatively little dependable information on documenting members of the Bibionidae as significant pollinators outside southern Africa, although various small flies in the suborder Nematocera, to which the family Bibionidae belongs, are known to pollinate plant species with small, dull-colored but musty-scented flowers (Proctor et al., 1996). Nematoceran flies have, however, been considered inefficient pollinators, and low fruit set has been noted in some species visited by these insects. An exception is *Disa obtusa*, which showed excellent fruit set (Johnson & Steiner, 1994). In addition, bibionid flies on flowers of *Viola* L. species in British woodlands are regarded as nectar thieves. Their foraging behavior and contact with anthers was distinct from that of pollinating syrphids (*Rhingia* Scopoli spp.) and bee flies (Bombyliidae) that dispersed *Viola* pollen in conjunction with foraging, native Hymenoptera and Lepidoptera (Beattie, 1971, 1972, 1978). Bibionids have also been recorded as part of a suite of pollinators in species of the New Zealand mountain flora (Primack, 1983), and in the high northern Cascades of the United States (Shaw & Taylor, 1986). In another instance, however, species of *Bibio* were reported by Cruden (1972) to be the sole pollinators of *Nemophila otomaria* Fisch. & Mey. (Hydrophylla-

ceae), in coastal northern California, which is elsewhere pollinated by bees.

The literature referring to the pollination of flowers by small flies, some with comparatively elongated mouthparts, has accumulated to the point where it can no longer be dismissed as speculation based on incomplete observations. Pollination within the complicated spathe and spadix complex within some species of Araceae is effected by a range of gnats and midges (Proctor et al., 1996), and pollination by microdipterans (body length less than 6 mm) occurs in both epiphytic tropical and terrestrial temperate species in the Orchidaceae. A few orchid species offer these insects nectar (e.g., *Acianthus* R. Br., *Genoplesium* R. Br.) while the majority appear pollinated by deceit (e.g., *Corybas* Salisb. and *Pterostylis* R. Br.; see Dressler, 1981; Dafni & Bernhardt, 1989). Microdipterans have also been implicated in the pollination of tropical rainforest grasses, e.g., *Olyra, Pariana,* which grow in the understory where there is no air movement to effect wind pollination, typical for Poaceae (Soderstrom & Calderón, 1971). To date, insect pollination in Poaceae remains largely speculative, and critical observations relating to rewards and attractants and the effectiveness of any insect species as a pollen vector are lacking. Pollen-eating and/or pollen-foraging insects often consume the pollen of wind-pollinated flowers. For example, small worker bees (*Trigona* sp.) were observed by one of us (PB, unpublished) foraging on pollen of flowering grasses in weedy neglected lots in San Salvador, but were never seen to contact the stigmas. In contrast, commercial production of the seed of *Theobroma cacao* increases when tropical plantations encourage breeding colonies of two families of midges (Young, 1994). References to small-bodied flies in the families Cecidomyiidae, Ceratopongonidae, Drosphilidae, Chloropidae (Bishop, 1996), Mycetophilidae, and Phoridae as pollinators currently outnumber those belonging to the Bibionidae.

Finally, while radial symmetry dominates in flowers pollinated by microdipterans, it is noteworthy that *Melasphaerula* shares bilateral symmetry with all the orchid genera discussed above, as well as *Tolmiea menziesii* (Pursh) Torr. & A. Gray (Saxifragaceae) (Goldblatt et al., 2004).

Plants pollinated almost exclusively by these microdipterans share some characters in common, and it may be possible to interpret and define a true syndrome in the future. With the exception of the much inflated "window flowers" of mimetic orchids in the genus *Pterostylis* (Bernhardt, 1994), the majority have a perianth circumference measured usually in millimeters, even when they mass their tiny florets together to make thickened-fleshy spikes, as in the Araceae. Contrasting pigmentation patterns emphasizing bright yellows, oranges, reds, and/or blues through light purple or violet are uncommon. The majority of flowers are described as white, often contrasting with green or greenish yellow or in various dull shades of rust, iodine, and maroon. Odors are unusually variable, ranging from bitter to musty or foetid, with fragrances reminiscent of mildew, mushrooms, ripe fruit, or citrus peel. These species bloom when their sites are seasonally or perpetually damp or humid. Many are found in woodland or forest as herbs, lianas, or shubs blooming under larger shrubs or in the shade of the canopy.

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POLYPLOIDY IN THE FLORA OF THE HENGDUAN MOUNTAINS HOTSPOT, SOUTHWESTERN CHINA[1]

Ze-Long Nie,[2] Jun Wen,[3] Zhi-Jian Gu,[2] David E. Boufford,[4] and Hang Sun[2]

ABSTRACT

The Hengduan Mountain region is located at the eastern end of the Himalayan range and in the southeastern corner of the Qinghai-Tibet Plateau in eastern Asia. It is probably the richest temperate region in the world biologically, with about 8000 species recorded from the 500,000 km² region. A high rate of polyploidy was expected in the Hengduan Mountains because of the unusually high species diversity and endemism, the widespread alpine environment in this region, and the importance of polyploidy in plant evolution. Chromosome numbers for 552 taxa of native Hengduan angiosperms were obtained from published literature. If the criterion of infrageneric polyploidy is used (i.e., the possession of three or more basic chromosome sets in a nucleus), the frequency of polyploidy is only 22%. It is 37% and 58% if taxa with haploid chromosome number $n = 14$ or more, or $n = 11$ or more are considered to be polyploids, respectively. Several highly diversified groups such as *Aconitum* and *Delphinium* also show a low proportion of polyploidy (18.6% and 0%, respectively) in the Hengduan Mountains. Examples from other large plant groups (e.g., *Saxifraga*, *Ligularia*, and *Cremanthodium*) and endemic genera (e.g., *Solms-laubachia*, *Tibetia*, and *Nomocharis*) again indicated that polyploidy, especially infrageneric polyploidy, may have played a minor role in the evolutionary diversification of these plants in the Hengduan Mountains.

Key words: chromosome number, diversification, Hengduan Mountains, Hotspot, polyploidy.

The Hengduan Mountains are located at the eastern end of the Himalayan range and in the southeastern corner of the Qinghai-Tibet Plateau, the highest and youngest plateau in the world. The region comprises more than 500,000 km² of temperate to alpine mountains in southwestern China and is bounded in the northwest by the dry Qinghai-Tibet Plateau, in the north by the Tao River of southern Gansu, and in the east by the Sichuan Basin and the plateau of eastern Yunnan. It also includes small portions of extreme northern Myanmar and extreme eastern India. About 8000 species of flowering plants have been recorded from this region (X. W. Li & Li, 1993; W. T. Wang et al., 1993, 1994), making it one of the two most speciose floristic subregions of the Sino-Himalayan Floristic Region, the other being the East Himalayan subregion (Wu, 1979, 1988; X. W. Li, 1994). The region is also renowned as the home of the giant panda (Wu, 1988). Based on a series of expeditions to the region during 1981–1983 organized by the Chinese Academy of Sciences (Wu, 1988), W. T. Wang et al. (1993, 1994) and X. W. Li and Li (1993) published a preliminary appraisal of the flora that documented its high levels of species diversity and endemism. Although the Hengduan Mountains are still poorly known to the western scientific community, they are biologically among the world's richest and most diverse regions (Boufford & van Dyck, 1999) and have recently been recognized as the biologically richest temperate region in the world, characterized by the occurrence of some of

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[2] Kunming Institute of Botany, Chinese Academy of Sciences, Kunming, Yunnan 650204, People's Republic of China. hsun@mail.kib.ac.cn (H. Sun).

[3] Department of Botany, Field Museum of Natural History, 1400 S. Lake Shore Dr., Chicago, Illinois 60605-2496, U.S.A., and Laboratory of Systematic and Evolutionary Botany, Institute of Botany, Chinese Academy of Sciences, Nanxincun 20, Xiangshan, Beijing 100093, People's Republic of China. wen@fieldmuseum.org; current address: Department of Botany, National Museum of Natural History, MRC-166, Smithsonian Institution, P.O. Box 37012, Washington, D.C. 20013-7012, U.S.A.

[4] Harvard University Herbaria, 22 Divinity Avenue, Cambridge, Massachusetts 02138-2020, U.S.A. boufford@oeb.harvard.edu.

the world's most distinctive species, such as *Acanthochlamys bracteata* P. C. Kao (Velloziaceae), *Sinadoxa corydalifolia* C. Y. Wu et al. (Adoxaceae), *Salweenia wardii* E. G. Baker (Fabaceae), and *Takakia ceratophylla* (Mitt.) Grolle (Bryophyta). Other floristic characteristics of the range include great regional radiations within a large number of plant groups, and the occurrence of a large number of relict plant lineages (Ying & Zhang, 1984; Wu, 1988; H. S. Wang, 1989; Wilson, 1992; X. W. Li & Li, 1993; Ying et al., 1993; H. S. Wang & Zhang, 1994; Boufford & van Dyck, 1999; H. Sun, 2002a, b; H. Sun & Li, 2003). The area was previously included in the Eastern Himalayan "hot spot" (Myers, 1988; Wilson, 1992), but more recently has been referred to as the South-Central China Hotspot (Myers et al., 2000) or the Hengduan Mountains Hotspot (Boufford & van Dyck, 1999). This Hotspot is a focus for studies of relationships between florogenesis and plate tectonics, on the origins of the north temperate flora, including the floras of eastern Asia, North America, and Europe, and on the evolution of seed plants in general (Wu, 1988).

Polyploidy, the possession of three or more basic chromosome sets in nuclei (Bennett, 2004), has long been recognized as a prominent force in the evolutionary diversification of plants (Winge, 1917; Darlington, 1937; Stebbins, 1940, 1950, 1971; Grant, 1981; Levin, 2002), especially ferns (Wagner, 1980; Werth et al., 1985) and flowering plants (Lewis, 1980; Soltis & Soltis, 2000; Wendel, 2000). This phenomenon occurs in up to 80% of all angiosperm species and is considered to be one of the most important cytogenetic mechanisms in plant evolution (Masterson, 1994; Levin, 2002), especially in facilitating rapid speciation (Hiremath & Salimath, 1991).

At the beginning of this research, our working hypothesis was that a high proportion of polyploids occurs in the angiosperm flora of the Hengduan Mountains. Below we outline the reasoning behind this hypothesis and provide a general introduction on the physical and biological characteristics of the Hengduan Mountains Hotspot.

The Hengduan Mountains are geologically young, yet possess an extremely rich flora both in terms of overall species diversity and endemics. The Hengduan Mountains rose relatively rapidly from sea level to the present high mountains (up to 7600 m) with rugged and dissected topography following the collision of the Eurasian and Indian plates about 50 million years ago (Patriat & Achache, 1984; C. S. Wang & Ding, 1998; Tao, 1992, 2000). The most common mechanism for rapid speciation in plants is through polyploidy (Grant, 1981). Recent studies in several plant groups have revealed that the genesis of allopolyploidy under both synthetic and natural conditions is often accompanied by rapid genetic and sometimes evolutionarily conserved epigenetic changes (B. Liu et al., 1998; Ozkan et al., 2001; B. Liu & Wendel, 2003; Osborn et al., 2003; Soltis et al., 2004). The capacity of angiosperms to form new combinations via polyploidy may help explain rapid diversification and high endemism in a given region with high biodiversity. Polyploidization might thus account for the high species diversity and endemism in the Hengduan region.

In regions such as the Hengduan Mountains with highly diversified floras, a high frequency of polyploidy would also be expected because of the crucial role of polyploidy in plant speciation (Grant, 1981). Polyploids can have more than two different alleles at any given locus. The intrinsic advantages of heterozygosity may be a key factor in the growth, performance, and adaptability of a polyploid (Grant, 1981; Levin, 1983; Ramsey & Schemske, 1998, 2002; Soltis et al., 2004). Polyploid populations often demonstrate extensive genomic rearrangement including the origin of novel regions of DNA (Song et al., 1995; Arnold, 1997).

Alpine and arctic floras have been reported to have high frequencies of polyploidy (Hanelt, 1966; Löve & Löve, 1967, 1975; Ohba, 1988; Abbott & Brochmann, 2003; Brochmann et al., 2004). Likewise, polyploids are more common in cold climates associated with harsh environmental conditions (Löve & Löve, 1949, 1967). Grant (1981) also suggested that disturbed habitats and stressful environments, which are often associated with cold climates, usually favor polyploidy. The great ecological amplitude that polyploid species can exhibit gives them a high degree of buffering against environmental changes over long periods of time due to glaciation, mountain building and degradation, and overall fluctuations in climate (Stebbins, 1971; Grant, 1981). The Hengduan region has extensive alpine areas. Environmental extremes such as cold and severe climate, and nutrient stress in high latitude or altitude areas have been suggested to increase the frequency of $2n$ gamete formation (Thompson & Lumaret, 1992; Levin, 2002), which leads to polyploidy.

Polyploids have been suggested to be more adaptive in disturbed or novel niches than their diploid progenitors (Ehrendorfer, 1980; Grant, 1981; Stebbins, 1985; Morton, 1993; Otto & Whitton, 2000; Levin, 2004). The Tertiary Himalayan orogeny has led to changes in the climate and topography of the

Hengduan Mountains (J. J. Li et al., 1995; Shi et al., 1998), whose uplifting and the advance and retreat of ice sheets and glaciers may have provided opportunities for the establishment of polyploids through hybridization and other mechanisms in the contact zones between existing species. The advantages and fitness polyploidy can bestow on organisms will be most effective when new habitats are being created and become available for colonization (Morton, 1993). Ehrendorfer (1980) also surveyed various plant communities to determine polyploid frequency in the flora of lower Austria, and found that the highest proportion of polyploid species was found in disturbed areas.

The objectives of this paper are to: (1) present a comprehensive review of chromosome numbers for the flora of the Hengduan Mountains, (2) calculate the frequency of polyploidy in this region and in exemplar taxa, and (3) test the hypothesis that polyploidy is important in the evolutionary diversification of its rich angiosperm flora.

Methods and Terminology

For each taxon (including species and subspecies), chromosome numbers were recorded from published reports. Several chromosome atlases were also consulted (Darlington & Wylie, 1955; Bolkhovskikh et al., 1969; Moore, 1973, 1974, 1977; Goldblatt, 1981, 1984, 1985, 1988; Goldblatt & Johnson, 1990, 1991, 1994, 1996, 1998, 2000, 2003).

We employed three methods to evaluate polyploids. First, taxa with three or more basic chromosome sets in nuclei are regarded as polyploids (Bennett, 2004), i.e., as resulting from infrageneric polyploidy (Stebbins, 1950). The second method recognizes polyploidy based on the criterion of haploid number $n = 14$ or more for statistical purposes (Grant, 1963, also see 1981: 296). Goldblatt (1980) suggested a third method, arguing that Grant's (1963) estimate was too conservative, and proposed that taxa with haploid number $n = 11$ or more should be considered as polyploids. In our study, we have employed all three methods to estimate the incidence of polyploidy in the Hengduan region. We emphasize infrageneric polyploidy in our discussion, because we consider this measure to be the most accurate of the three. We also inferred the ploidal level for each taxon based on Stebbins's (1950) criterion (results shown in Appendix 1). A few taxa with both polyploid and diploid counts are treated as polyploids in our calculation.

In this paper, $2n$ refers to a taxon's somatic chromosome number and n to the gametic chromosome number regardless of the ploidy level, while x is the most probable base number. The large number of species and the paucity of taxonomic treatments for the study region made it difficult to assign previously published records to currently recognized taxa. We thus report chromosome numbers under the names that were originally published.

Frequency of Polyploidy in the Hengduan Mountains

Chromosome counts for 552 species and infraspecific taxa in 152 genera and 44 families from the Hengduan Mountains are shown in Appendix 1. Most taxa are representatives of genera that are taxonomically diversified and ecologically common in the region, such as *Rhododendron*, *Silene*, *Arenaria*, *Rubus*, *Ligularia*, *Delphinium*, *Poa*, *Astragalus*, *Saussurea*, *Aconitum*, *Primula*, *Gentiana*, and *Pedicularis*, all of which are characterized by regional radiation. Others, such as *Acanthochlamys*, *Beesia*, *Circaeaster*, *Dichotomanthes*, *Kingdonia*, *Nomocharis*, *Pomatosace*, *Przewalskia*, *Salweenia*, *Solms-laubachia*, and *Souliea*, are largely endemics to the region. At present no chromosome counts are available for certain large families, such as Lamiaceae, Cyperaceae, and Crassulaceae.

When polyploidy is calculated based on three or more basic chromosome sets in nuclei recorded in a genus (infrageneric polyploidy), only 22% (124/552) of the angiosperm taxa sampled in the Hengduan Mountains are polyploids. Using this same method, 30%–35% are estimated to be polyploids for all flowering plants whose chromosome numbers have been counted (Stebbins, 1950) and 36% for monocots (Goldblatt, 1980: 225).

Based on the criterion that haploid number $n = 14$ or more denotes polyploidy sensu Grant (1963, 1981), 37% (204/552) of the angiosperm taxa from the Hengduan Mountains are polyploids (Table 1). These values are relatively low compared with previous estimates. Grant (1963) reported that 47% of the 17,138 species of flowering plants he sampled were polyploids. According to the method of Goldblatt (1980) with $n = 11$ or above as polyploids, 58% (322/552) of the angiosperm taxa in the Hengduan region are polyploids. Using the same criterion, Goldblatt (1980) reported that 68% of the 10,580 species of monocots he surveyed were polyploids.

Comparisons with Other Regions

Because of the limited sample size of our chromosome data (ca. 6.9% of the estimated 8000 species present in the Hengduan Mountains), we com-

Table 1. Polyploidy statistics of angiosperms in the Hengduan Mountains based on three methods: (a) infrageneric polyploids—taxa with three or more base chromosome number sets (Stebbins, 1950; Bennett, 2004); (b) haploid number $n = 14$ or more (Grant, 1963); (c) $n = 11$ or more (Goldblatt, 1980).

	Total species (%)	Infrageneric polyploidy Species number (%)	Polyploidy ($n \geq 14$) Species number (%)	Polyploidy ($n \geq 11$) Species number (%)
All species sampled	552	124 (22)	204 (37)	322 (58)
Endemic species	183 (33)	29 (16)	49 (27)	89 (49)

pared our findings with chromosome data for the plants of Pakistan. Pakistan is located on the western end of the Himalayan range. The chromosome data from Pakistan are based on a larger sample size, i.e., 1777 species and infraspecific taxa sampled (34% of its total angiosperm flora). As shown in Table 2, the frequency of polyploidy in Pakistan is similar to what we found for the Hengduan Mountains, with 29% infrageneric polyploidy, and 44% ($n = 14$ or more) or 63% ($n \geq 11$) based on the two methods for estimating polyploidy, as calculated using data taken from Khatoon and Ali (1993). The similar incidence of polyploidy in these two regions may reflect a broader characteristic of polyploid distribution in the Himalayan range. Although the sample size in our study includes only a small proportion of the angiosperm flora of the Hengduan Mountains, it nevertheless provides good taxonomic and ecological representation. The available data suggest that the flora of the Hengduan Mountains is characterized by a relatively low frequency of polyploidy.

As indicated above, the frequency of polyploidy is higher in arctic floras than those at lower latitudes (Hanelt, 1966; Löve & Löve, 1975; Abbott & Brochmann, 2003). The frequency of polyploid species in the vascular flora of the arctic region as a whole is nearly 60% in the low arctic zone, but 70% in the high arctic and as high as 80% in high-arctic endemics (Löve & Löve, 1975). Brochmann and Steen's (1999) research on the isolated arctic archipelago of Svalbard, which was almost completely ice-covered during the last glaciation, showed that nearly 80% of the 161 native species are polyploids. A recent review on arctic plants based on 1719 taxa showed that the majority (60.7%) are polyploids, especially for arctic specialist taxa (73.7%) (Brochmann et al., 2004).

Löve and Löve (1967) pointed out that the frequency of polyploidy is significantly high in the alpine zone, as on Mt. Washington in the White Mountains of New Hampshire, where 63.6% of the alpine taxa of vascular plants are polyploids. Another example is from the flora of the Cameroon Mountains (Morton, 1993), which shows a frequency of 52.9%, higher than generally reported (sensu Grant, 1981). Hanelt (1966) gave percentages ranging from 45% to 85% polyploids in various high mountain floras in Eurasia, the Americas, and New Guinea.

Our finding of only 22% polyploidy in the angiosperm flora of the Hengduan Mountains based on the same method of calculation (Stebbins, 1950) stands in sharp contrast with these earlier results.

Table 2. Comparison of frequency of polyploidy among selected regions or plant groups.

	Reference	Infrageneric polyploidy, %	Polyploidy ($n \geq 14$), %	Polyploidy ($n \geq 11$), %
Hengduan Mountains		22	37	58
Pakistan	Khatoon & Ali (1993)	29	44	63
Monocots	Goldblatt (1980)	36		68
Angiosperms	Stebbins (1950)	30–35		
	Grant (1963, 1981)		47	
High mountain floras	Hanelt (1966)	45–85		
Cameroon Mountains	Morton (1993)	52.9		
Mt. Washington	Löve & Löve (1967)	63.6		
Arctic flora	Löve & Löve (1975)	60–80		
	Brochmann et al. (2004)	60.7		
Svalbard	Brochmann & Steen (1999)	ca. 80		
Juan Fernandez Islands	Sanders et al. (1983)		75	
Hawaii	Carr (1998)		80	

A similar survey on Chihuahuan Desert flora showed that a relatively low frequency of 17.8% polyploidy occurs among the gypsophilic species compared to 32.7% polyploidy for the non-gypsum vegetation (Powell & Sloan, 1975). Further chromosome reports on some species from the Hohxil region of Qinghai, a harsh, cold, uninhabited, alpine desert at an average elevation of 5000 m near the center of the Qinghai-Xizang Plateau, also showed that most plants there are diploids (Y. P. Yang & Wu, 1993).

Several studies using the more inclusive criterion that taxa with gametic numbers of $n = 14$ and above are regarded as polyploids (Grant, 1963) have found higher levels of polyploidy than the 58% we estimated for the Hengduan region. For example, Sanders et al. (1983) reported 75% polyploidy for the flora of the Juan Fernandez Islands, and Carr (1998) reported 80% for Hawaiian plants.

Polyploidy in Representative Taxa

We expected to find a high level of polyploidy before we began this study, but it seems that polyploidy is not common in the Hengduan Mountains based on regional cytological statistical comparisons. This result is even more pronounced when one considers the frequency of polyploidy in several representative taxa from the Hengduan Mountains Hotspot.

HIGHLY DIVERSIFIED GROUPS

Aconitum and *Delphinium* are two closely related genera of Ranunculaceae in the tribe Delphineae and are widely distributed in north temperate areas. About half of the species of *Aconitum* and more than 63% of the species of *Delphinium* are found in the Hengduan Mountains (Q. E. Yang et al., 1989). The species in these two genera are highly diversified in the region, with both primitive and advanced representatives, including many local endemics (X. W. Li & Li, 1993; Q. E. Yang, 1996). The cytological data reveal that of 43 species in *Aconitum* in the Hengduan region (41% of the total 104 species), 30 are endemic to the area, and only eight are polyploids (18.6%). There are no polyploids among the 23 species (11 endemics) of *Delphinium* reported (32% of the total 71 species in the region). However, in Simon et al.'s (1999) comprehensive chromosome survey of Delphineae, which included about 40% of species in the tribe, 48% and 31% of *Aconitum* and *Delphinium* species were found to be polyploids, respectively. These figures are much higher than our estimates from the Hengduan region. The high diversity of these genera in this region has resulted mainly from speciation within diploid lineages.

Ligularia and *Cremanthodium* (Asteraceae) are two related genera that are also highly diversified in the Hengduan Mountains (Liu, 2004). *Ligularia* has 129 species in the region, with about 100 native and 60 endemic. This genus is morphologically diverse and has members in a variety of habitats, from forests to high alpine meadows, ranging from 1000 to 4000 m in altitude, although most species are found in the mountains (S. W. Liu et al., 1994). *Cremanthodium* comprises 67 species growing in alpine meadows, largely in the Hengduan Mountains and on the Qinghai-Tibet Plateau. Although these genera do not qualify for Stebbins's (1950) definition of infrageneric polyploidy, their high haploid chromosome numbers of $n = 30$ and $n = 29$ suggest ancient polyploidizations. Variation of karyotype structure at the diploid level seems to be the predominant feature in these groups, and sympatric speciation via hybridization and polyploidization has played a minor role in their species diversity (J. Q. Liu, 2004).

A similar phenomenon can be seen in several other groups occurring around or within the Himalaya and Qinghai-Tibet Plateau. *Saxifraga* (Saxifragaceae) is widely distributed in the temperate zone of the Northern Hemisphere and is one of the most important components of the alpine flora of the Himalayan region (Ohba, 1986). In particular, some species are quite diverse in the high alpine region of the Himalaya as well as in the Hengduan Mountains. In the Hengduan Mountains, four of the nine species reported are polyploids (44.4%). However, cytological studies of *Saxifraga* in the Himalayas by Wakabayashi and Ohba (1988) showed that diploids prevail and polyploids comprise only 17% of the species. Polyploidy thus may not have played an important role in the diversification of *Saxifraga* in the Himalayan range (Wakabayashi & Ohba, 1988).

ENDEMIC TAXA

High levels of endemism are a major feature of the flora of the Hengduan Mountains. About 37.7% of the angiosperms are endemic or mainly restricted to this area (X. W. Li & Li, 1993). Of the 552 taxa sampled, 33% are endemic to the Hengduan region (Table 1), a proportion similar to that of the total angiosperms in the region. But infrageneric polyploidy is particularly low among endemics (just 16%). Below we discuss several endemic genera to illustrate this phenomenon.

The nine species of *Solms-laubachia* (Brassica-

ceae) are nearly restricted to scree slopes and rocky crevices at altitudes of 3400–5700 m in the Hengduan Mountains (Al-Shehbaz & Yang, 2001; Yue et al., 2004). All species are $2n = 14$, although one species (*S. pulcherrima* Muschl.) has a tetraploid cytotype (Yue et al., 2003, 2004). Speciation within *Solms-laubachia* may have been the result of primarily intrachromosomal variation at the diploid level, and the genus probably evolved within the Himalayan-Hengduan Mountains instead of migrating from other regions (Yue et al., 2004).

Another example is the small, localized, nearly endemic genus *Tibetia* (Fabaceae). This genus apparently differentiated from the widely distributed north temperate *Gueldenstaedtia* and became adapted to the alpine environment (Tsui, 1979; Nie et al., 2002) as the Hengduan Mountains uplifted. The cytological studies of Nie (2002), Nie et al. (2002), and D. K. Yang (2002) show that the species of *Tibetia* have all evolved at the diploid level of $2n = 16$, but with alterations of their karyotypes. These authors suggest the importance of allopatric speciation at the diploid level in *Tibetia* in the Hengduan Mountains.

Nomocharis (Liliaceae), comprising ca. 10 species with the Sino-Himalayan distribution pattern, is restricted to the Hengduan Mountains and the southeastern edge of the Tibetan Plateau. All its members are not infrageneric polyploids, with $2n = 24$, and appear to have diversified at the diploid level after ancient polyploidization (Xie et al., 1992). Other taxa, such as *Salweenia* (Q. X. Zhou et al., 2000), *Beesia* (Q. E. Yang et al., 1995), and *Kingdonia* (Z. Y. Zhang, 1982), are likewise all diploids that have developed and become localized in the Hengduan Mountains area.

Evolution of High Species Diversity in the Hengduan Mountains Hotspot

If polyploidy did not play a major role in the evolution of Hengduan plants, what other mechanisms might have shaped the substantially high species diversity and endemisms in the region? Below we propose a few hypotheses based on physical and historical factors.

Alpine plants survive under the environmental conditions they encounter because of adaptive features such as cushion or rosette habit, pubescence, and coriaceous leaves (Chaverri-Polini, 1998; Körner, 2003). Morphological differentiation can be accumulated in a relatively short period under certain alpine environments through natural selection, without drastic genetic or chromosomal divergence. For example, *Sinadoxa*, an endemic monotypic genus of Adoxaceae from the Hengduan region, is closely related to *Adoxa* (J. Q. Liu et al., 2000b), but is morphologically very distinct, despite low ITS sequence divergence (3.4%), which suggests a recent origin of *Sinadoxa*. Both genera have the same chromosome number of $2n = 36$ and a similar karyotype, and the initial differentiation between them might have resulted from allopatric isolation when the first large-scale uplifting of the Qinghai-Tibet Plateau occurred about 3.4–1.7 million years ago (J. Q. Liu et al., 1999, 2000b).

Geographical and ecological heterogeneity may have played an important role in the diversification of plants in the Hengduan Mountains. Most parts of the region are characterized by a series of parallel mountain ranges dissected by deep river valleys that run from north to south, which present physical barriers to gene flow. The high speciation rate in the Hengduan flora may also be due to highly varied local climates that result from geographic differences in the mountains. The wide diversity of climates combined with local differences in geomorphological, edaphic, and ecological features may have generated distinct niches for different species. *Rhododendron* (Ericaceae), for example, is the largest genus in the region with about 220 species extending throughout the Hengduan area, but most species have highly localized distributions. Both diploids and polyploids are common among *Rhododendron* in the Hengduan Mountains, with a high base chromosome number of $x = 13$ (Darlington & Wylie, 1955; Gao, 2002). The radiation of *Rhododendron* in this region is perhaps related to geographic heterogeneity in conjunction with polyploidy.

Animals such as insects may have played a vital role in the dispersal as well as the evolution of reproductive isolation of some groups in the region. *Pedicularis* is a circumpolar genus of Scrophulariaceae, consisting of approximately 500 species, with about 200 occurring in the Hengduan Mountains, making it the second largest genus of angiosperms in the region (X. W. Li & Li, 1993). *Pedicularis* shows extreme variation in floral morphology that is correlated with specific mechanisms of pollination involving a diverse group of insects. Chromosome numbers of *Pedicularis* recorded in the Hengduan Mountains are $2n = 14$ and 16 (J. Cai et al., 2004), suggesting that the evolution has taken place at the diploid level and that diversification is perhaps facilitated by the behavior of pollinators.

Climatic changes during the Pleistocene glacial and interglacial periods may have resulted in the formation of many refugia in the region; these re-

fugia may have served as shelters for a rich diversity of species, as well as sources for dispersion to neighboring areas during the warm interval. The arctic and Tethyan Tertiary floras also served as a source of the floristic development of the region, with the existence of migration routes for plants from the north to the south and vice versa (H. Sun, 2002a, 2002b; H. Sun & Li, 2003).

Conclusions

Polyploidy (especially infrageneric polyploidy) is not common in the alpine flora of the Hengduan Mountains Hotspot based on our cytological statistical analysis. This finding is further strengthened by case studies of representative taxa in the region. High levels of speciation activities in the Hotspot are probably attributable at least in large part to the geographic, climatic, and geological heterogeneity that resulted from the Tertiary Himalayan orogeny and Cenozoic ice-age cycles. Further investigations, particularly of taxa characteristic of the area, are needed to (a) further test our findings of low frequency of polyploids in the Hengduan region in a phylogenetic framework, (b) examine other prominent evolutionary forces involved in speciation in the Hotspot, and (c) explore the possible reasons for the apparently low rate of formation and/or survival of polyploid species. We hope this cytological study will stimulate further chromosomal and evolutionary work on the Hengduan Mountains Hotspot, and on other conservation hotspots as well.

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Appendix 1. Chromosome reports and ploidal levels in angiosperms of the Hengduan Mountains. $2n$ = somatic chromosome number; n = gametic or haploid chromosome number; x = chromosome base number; GS = Gansu; QH = Qinghai; SC = Sichuan; XZ = Xizang; YN = Yunnan Province, China.

Taxon	Locality	n	$2n$	Ploidy	Reference
ADOXACEAE					
Sinadoxa corydalifolia Z. Y. Wu, Z. L. Wu & R. F. Huang	QH: Yushu		36	$2x$	X. F. Lu et al. (2002)
Tetradoxa omeiensis (Hara) C. Y. Wu	SC: Mt. Emei, 2300 m		36	$2x$	H. X. Liang (1986)
APIACEAE					
Angelica chinghaiensis Shan ex K. T. Fu	SC: Songpan, 3500 m		44	$4x$	Z. H. Pan et al. (1991)
A. dielsii H. Boissieu	SC: Songpan, 3000 m		22	$2x$	Z. H. Pan et al. (1991)
A. laxifoliata Diels	SC: Hanyuan, 1900 m		22	$2x$	Z. H. Pan et al. (1991)
A. maowenensis C. Q. Yuan & R. H. Shan	SC: Songpan, 2800 m		22	$2x$	Z. H. Pan et al. (1991)
A. omeiensis C. Q. Yuan & R. H. Shan	SC: Mt. Emei, 2100 m		22	$2x$	Z. H. Pan et al. (1991)
A. setchuenensis Diels	SC: Songpan, 2800 m		22	$2x$	Z. H. Pan et al. (1991)
A. sinensis (Oliv.) Diels	SC: Songpan, 2900 m		22	$2x$	Z. H. Pan et al. (1991)
Bupleurum marginatum Wall. ex DC. var. *stenophyllum* (Wolff) Shan & Y. Li	YN: Heqin	7		$2x$	Chin et al. (1989)
Heracleum candicans Wall.	SC: Songpan		22	$2x$	X. J. He et al. (1994)
H. franchetii M. Hiroe	SC: Xiaojin		22	$2x$	X. J. He et al. (1994)
H. hemsleyanum Diels	SC: Lixian		22	$2x$	X. J. He et al. (1994)
H. henryi H. Wolff	YN: Lushui	22		$4x$	X. J. He et al. (1994)
H. millefolium Diels	SC: Songpan		22	$2x$	X. J. He et al. (1994)
H. millefolium Diels var. *longilobum* C. Norman	SC: Songpan		22, 24	$2x$	X. J. He et al. (1994)
H. obtusifolium Wall.	SC: Wenchuan		22	$2x$	X. J. He et al. (1994)
H. stenopterum Diels	SC: Songpan		22	$2x$	X. J. He et al. (1994)
H. vicinum H. Boissieu	SC: Wenchuan		22	$2x$	X. J. He et al. (1994)
H. wolongense F. T. Pu & X. J. He	SC: Wenchuan		22	$2x$	X. J. He et al. (1994)
H. yungningense Hand.-Mazz.	SC: Xiaojin		22	$2x$	X. J. He et al. (1994)
Ligusticum acuminatum Franch.	SC: Xiaojin		22	$2x$	Z. H. Pan et al. (1985)
L. brachylobum Franch.	YN: Heqin	11		$2x$	Chin et al. (1989)
L. pteridophyllum Franch. ex Gliver	YN: Dali	11		$2x$	Chin et al. (1989)
Physospermopsis rubrinervis (Franch.) C. Norman	YN: Lijiang	11		$2x$	Chin et al. (1989)
Pimpinella flaccida C. B. Clarke	YN: Binchuan	10		$2x$	Chin et al. (1989)
Pleurospermum angelicoides Benth. ex C. B. Clarke	YN: Lijiang		22	$2x$	Chin et al. (1989)
P. rivulorum (Diels) K. T. Fu & Y. C. Ho	YN: Lijiang		22	$2x$	Chin et al. (1989)
Tongoloa elata H. Wolff	YN: Dali	11		$2x$	Chin et al. (1989)
Trachyspermum scaberulum (Franch.) H. Wolff var. *ambrosiifolium* (Franch.) R. H. Shan	YN: Binchuan	9		$2x$	Chin et al. (1989)
ARACEAE					
Acorus calamus L.	YN: Zhongdian		66	$6x$	H. Wang et al. (2001)
Amorphophallus bannanensis H. Li	YN: Gongshan, 1280 m		26	$2x$	Gu et al. (1992)
Arisaema biauriculatum W. W. Sm.	YN: Gongshan, 2600 m		28	$2x$	Gu et al. (1992)
	XZ: Motuo, 1100 m		28	$2x$	Gu & Sun (1998)
A. dulongense H. Li	YN: Gongshan, 2600 m		26	$2x$	Gu et al. (1992)

Appendix 1. Continued.

Taxon	Locality	*n*	2*n*	Ploidy	Reference
A. erubescens Schott	YN: Gongshan, 2300 m		56	4*x*	Gu et al. (1992)
A. heterophyllum Blume	SC: Mt. Emei		28	2*x*	Murata & Iijima (1983)
A. lobatum Engl.	SC: Mt. Emei, 1700 m		56	4*x*	Hong & Zhang (1990)
Colocasia gaoligongensis H. Li & C. L. Long	YN: Tengchong, 3700 m		28	2*x*	Z. Y. Yang et al. (2003)
Remusatia hookeriana Schott	YN: Gongshan, 2800 m		28	2*x*	Gu et al. (1992)
	YN: Dali		28	2*x*	Long et al. (1989)
R. vivipara Schott	YN: Dali		42	3*x*	H. Li & Hay (1992)
	YN: Dali		42	3*x*	Long et al. (1989)
Sauromatum gaoligongense Z. L. Wang & H. Li	YN: Baoshan, 2290 m		26	2*x*	Bian et al. (2001)
ASTERACEAE					
Ajania myriantha (Franch.) Ling ex C. Shih	SC: Wenchuan, 1400 m		18, 36	2*x*, 4*x*	Kondo et al. (1995)
A. przewalskii Poljakov	SC: Lixian, 3800 m		36	4*x*	Kondo et al. (1992)
A. ramosa (Chang) C. Shih	SC: Kanging, 3100 m		18	2*x*	Kondo et al. (1992)
A. tenuifolia (Jacq.) Tzvelev	SC: Kangding, 4150 m		36	4*x*	Kondo et al. (1992)
Aster diplostephioides Benth. & Hook. f.	QH: Yushu, 3850 m		18	2*x*	J. Q. Liu (1999)
A. souliei Franch.	QH: Yushu, 3950 m		18	2*x*	J. Q. Liu (1999)
A. yunnanensis Franch. var. *labrangensis* (Hand.-Mazz.) Y. Ling	QH: Yushu, 3850 m		18	2*x*	J. Q. Liu (1999)
Cremanthodium brunneopilosum S. W. Liu	SC: Hongyuan, 3900 m		58	2*x*	J. Q. Liu et al. (2001)
C. discoideum Maxim.	QH: Maduo, 4900 m		58	2*x*	J. Q. Liu et al. (2001)
C. ellisii (Hook. f.) S. Kitamura	QH: Maduo, 4800 m		58	2*x*	Huang et al. (1996a)
	QH: Yushu, 4500 m		58	2*x*	J. Q. Liu et al. (2001)
C. humile Maxim.	QH: Maduo, 4800 m		116	4*x*	Huang et al. (1996a)
	QH: Maqing, 4300 m		60	2*x*	J. Q. Liu et al. (2001)
C. lineare Maxim.	QH: Maduo, 4500 m		58	2*x*	J. Q. Liu et al. (2001)
C. microglossum S. W. Liu	QH: Yushu, 4700 m		58	2*x*	J. Q. Liu et al. (2001)
C. stenoglossum Ling & S. W. Liu	QH: Maduo, 5000 m		58	2*x*	J. Q. Liu et al. (2001)
Dendranthema glabriusculum (W. W. Sm.) C. Shih	SC: Zhaojue, 1950 m		54	6*x*	Kondo et al. (1998)
D. lavandulifolium (Fisch. ex Trautv.) Y. Ling & C. Shih	SC: Mt. Emei, 600 m		36	4*x*	J. W. Wang et al. (1993)
Erigeron annuus Pers.	SC: Baoxing, 1500 m	9		2*x*	Hong & Zhang (1990)
Gnaphalium affine D. Don	SC: Mt. Emei, 800 m	7		2*x*	Hong & Zhang (1990)
Ligularia cyathiceps Hand.-Mazz.	YN: Lijiang, 3600 m		58	2*x*	Y. Z. Pan et al. (2004a)
L. dentata (A. Gray) Hara	SC: Mt. Emei, 1500 m		58	2*x*	J. Q. Liu (2004)
L. dictyoneura (Franch.) Hand.-Mazz.	YN: Zhongdian		58	2*x*	Gong et al. (2001)
	YN: Lijiang, 3300 m		58	2*x*	J. Q. Liu (2004)
L. hookeri (C. B. Clarke) Hand.-Mazz.	YN: Dali		58	2*x*	Gong et al. (2001)
L. kanaitzensis (Franch.) Hand.-Mazz.	YN: Lijiang		58	2*x*	Gong et al. (2001)
L. liatroides (C. Winkler) Hand.-Mazz.	QH: Yushu, 3500 m		58	2*x*	J. Q. Liu (2004)
L. latihastata Hand.-Mazz.	YN: Lijiang		58	2*x*	Gong et al. (2001)
L. pleurocaulis Hand.-Mazz.	SC: Daocheng, 4500 m		58	2*x*	Y. Z. Pan et al. (2004a)
L. phyllocolea Hand.-Mazz.	YN: Ninglang, 3700 m		58	2*x*	Y. Z. Pan et al. (2004a)

Appendix 1. Continued.

Taxon	Locality	*n*	2*n*	Ploidy	Reference
L. purdomii (Turrill) Chittenden	SC: Hongyuan		58	2*x*	J. Q. Liu (2004)
L. stenocephala Matsum. & Koidzumi	YN: Dali		58	2*x*	Gong et al. (2001)
L. tangutorum Pojark.	QH: Maqin, 3200 m		58	2*x*	J. Q. Liu (2004)
L. tongolensis (Franch.) Hand.-Mazz.	YN: Zhongdian, 3200 m		58	2*x*	Y. Z. Pan et al. (2004a)
L. tsangchanensis (Franch.) Hand.-Mazz.	YN: Dali, 3000 m		58	2*x*	J. Q. Liu (2004)
L. vellerea Hand.-Mazz.	YN: Lijiang		58	2*x*	Gong et al. (2001)
L. virgaurea Mattf. ex Rehder & Kobuski	SC: Ruoergai		58	2*x*	J. Q. Liu (2004)
	QH: Maqing, 3700 m		87	3*x*	J. Q. Liu (2004)
L. yunnanensis (Franch.) Chang	YN: Dali, 3600 m		58	2*x*	Y. Z. Pan et al. (2004a)
Nannoglottis gynura (C. Winkler) Ling & Y. L. Chen	QH: Yushu, 3600 m		18	2*x*	J. Q. Liu et al. (2000a)
Nouelia insignis Franch.	YN: Zhongdian, 1988 m		54	6*x*	Peng et al. (2002)
Picris hieracioides L. subsp. *japonica* Krylv.	SC: Baoxing, 1800 m	5		2*x*	Hong & Zhang (1990)
Saussurea ceterach Hand.-Mazz.	QH: Nangqian, 3940 m		30	2*x*	Ho et al. (2002c)
S. eopygmaea Hand.-Mazz.	QH: Yushu, 4060 m		30	2*x*	Ho et al. (2002c)
S. gnaphalodes (Royle) Sch. Bip.	QH: BayanHarashan, 5200 m		48		Huang et al. (1996a)
S. tangutica Maxim.	QH: BayanHarashan, 5200 m		28	2*x*	Huang et al. (1996a)
S. wellbyi Hemsl.	QH: Maduo, 4700–4800 m		28	2*x*	Huang et al. (1996a)
Sonchus arvensis L.	SC: Mt. Emei, 800 m	9		2*x*	Hong & Zhang (1990)
Youngia erythrocarpa (Vaniot) Babc. & Stebbins	SC: Baoxing, 1500 m	8		2*x*	Hong & Zhang (1990)
Y. heterophylla (Hemsl.) Babc. & Stebbins	SC: Mt. Emei, 1200 m	6		2*x*	Hong & Zhang (1990)
BEGONIACEAE					
Begonia cavaleriei H. Lév.	YN: Eryuan		30	3*x*	Tian et al. (2002)
BERBERIDACEAE					
Diphylleia sinensis Li	YN: Zhongdian, 3200 m		12	2*x*	Ma & Hu (1996)
Dysosma versipellis (Hance) M. Cheng	SC: Mt. Emei, 805 m		12	2*x*	Ma & Hu (1996)
Sinopodophyllum hexandrum (Royle) Ying	YN: Zhongdian, 3200 m		12	2*x*	Ma & Hu (1996)
BIGNONIACEAE					
Incarvillea arguta Royle	YN: Zhongdian		22	2*x*	S. T. Chen et al. (2004)
I. berezovskii Batalin	SC: Maerkang		22	2*x*	S. T. Chen et al. (2004)
I. compacta Maxim.	SC: Shiqu		22	2*x*	S. T. Chen et al. (2004)
I. delavayi Bureau & Franch.	YN: Lijiang		22	2*x*	S. T. Chen et al. (2004)
I. dissectifolia Q. S. Zhao	SC: Yanyuan		22	2*x*	S. T. Chen et al. (2004)
I. forrestii Fletcher	YN: Zhongdian		22	2*x*	H. Xiao et al. (2002)

Appendix 1. Continued.

Taxon	Locality	*n*	2*n*	Ploidy	Reference
I. lutea Bureau & Franch.	SC: Daocheng		22	2*x*	S. T. Chen et al. (2004)
	YN: Lijiang		22	2*x*	H. Xiao et al. (2002)
I. mairei (H. Lév.) Grierson	YN: Zhongdian		22	2*x*	H. Xiao et al. (2002)
	YN: Dali		22	2*x*	S. T. Chen et al. (2004)
I. mairei (H. Lév.) Grierson var. *grandiflora* (Wehrhahn) Grierson	YN: Lijiang		22	2*x*	S. T. Chen et al. (2004)
I. sinensis Lam.	SC: Maerkang		22	2*x*	S. T. Chen et al. (2004)
I. younghusbandii Sprague	XZ: Nielamu		22	2*x*	S. T. Chen et al. (2004)
I. zhongdianensis Grey-Wilson	YN: Lijiang		22	2*x*	H. Xiao et al. (2002)
	YN: Zhongdian		22	2*x*	S. T. Chen et al. (2004)
BRASSICACEAE					
Solms-laubachia eurycarpa (Maxim.) Botsch.	YN: Deqin, 4600 m		14	2*x*	Yue et al. (2003)
	XZ: Basho, Yelashan		14	2*x*	Yue et al. (2004)
S. lanata Botsch.	XZ: Lhasa, Resela		14	2*x*	Yue et al. (2004)
S. linearifolia O. E. Schulz	YN: Deqin, 4310 m		14	2*x*	Yue et al. (2003)
S. minor Hand.-Mazz.	YN: Zhongdian, 4500 m		14	2*x*	Yue et al. (2003)
S. platycarpa (Hook. f. & Thomson) Botsch.	XZ: Nyenchengtang La				Yue et al. (2004)
S. pulcherrima Muschl.	YN: Lijiang, 4500 m		14	2*x*	Yue et al. (2003)
	YN: Lijiang		14	2*x*	Yue et al. (2004)
S. retropilosa Botsch.	SC: Xiangcheng, 4000 m		28	4*x*	Yue et al. (2003)
	XZ: Zuogong		14	2*x*	Yue et al. (2004)
S. xerophyta (W. W. Sm.) Comber	SC: Daocheng		14	2*x*	Yue et al. (2004)
Thlaspi arvense L.	SC: Baoxing, 2600 m	7		2*x*	Hong & Zhang (1990)
CAMPANULACEAE					
Adenophora lobophylla D. Y. Hong	SC: Jingchuan		34+2B	2*x*	K. Q. Wang & Ge (1998)
A. potanini Korsh.	SC: Baoxin		34	2*x*	K. Q. Wang & Ge (1998)
A. stricta Miq.	SC: Jingchuan		68	4*x*	K. Q. Wang & Ge (1998)
CAPRIFOLIACEAE					
Lonicera schneideriana Rehder	SC: Baoxing, 2600 m	9		2*x*	Hong & Zhang (1990)
CARYOPHYLLACEAE					
Psammosilene tunicoides W. C. Wu & C. Y. Wu	YN: Lijiang		28	2*x*	Y. Z. Pan et al. (2004b)
Stellaria neglecta Weihe	SC: Mt. Emei, 2100 m	22		4*x*	Hong & Zhang (1990)
CHLORANTHACEAE					
Chloranthus nervosus Collett & Hemsl.	YN: Yangbi, Meixi		30	2*x*	Kong (2000)
CUCURBITACEAE					
Gynostemma longipes C. Y. Wu	YN: Lijiang		44	4*x*	X. F. Gao et al. (1995)
Thladiantha davidii Franch.	SC: Pengxian, 1230 m		18	2*x*	J. Q. Li et al. (1993)
T. dentata Cogn.	SC: Nanchuan, 1650 m		18	2*x*	J. Q. Li et al. (1993)

Appendix 1. Continued.

Taxon	Locality	*n*	2*n*	Ploidy	Reference
T. lijiangensis A. M. Lu & Zhi Y. Zhang	YN: Lijiang, Longpan		18	2*x*	J. Q. Li et al. (1993)
T. nudiflora Hemsl. ex Forb. & Hemsl.	SC: Mt. Emei, 1650 m		18	2*x*	J. Q. Li et al. (1993)
DIOSCOREACEAE					
Dioscorea althaeoides Knuth	YN: Weixi	10	20	2*x*	Jiangsu Institute of Botany (1976)
D. collettii Hook. f.	SC: Emei	10	20	2*x*	Jiangsu Institute of Botany (1976)
D. deltoidea Wall.	YN: Deqin	10	20	2*x*	Jiangsu Institute of Botany (1976)
D. opposita Thunb.	SC: Mt. Emei		138–142	14*x*	Chin et al. (1985)
D. panthaica Prain & Burkill	YN: Lijiang	20	40	4*x*	Jiangsu Institute of Botany (1976)
D. parviflora C. T. Ting	YN: Yongsheng	10	20	2*x*	Pei et al. (1979)
D. zingiberensis C. H. Wright	YN: Liuku	10	20	2*x*	Jiangsu Institute of Botany (1976)
ELAEAGNACEAE					
Hippophae neurocarpa S. W. Liu & T. N. He	SC: Daocheng		24	2*x*	Y. L. Cao & Lu (1989)
H. rhamnoides L. subsp. *sinensis* Rousi	SC: Nanping		24	2*x*	Y. L. Cao & Lu (1989)
H. rhamnoides L. subsp. *yunnanensis* Rousi	YN: Zhongdian		24	2*x*	Y. L. Cao & Lu (1989)
H. tibetana Schlecht.	SC: Hongyuan		24	2*x*	Y. L. Cao & Lu (1989)
ERICACEAE					
Rhododendron mackenzianum Forrest	YN: Gongshan		26	2*x*	L. M. Gao (2002)
R. leptothrium Balf. f. & Forrest	YN: Weixi		26	2*x*	L. M. Gao (2002)
FABACEAE					
Astragalus acaulis Baker	SC		16	2*x*	S. M. Mu & Shue (1985)
A. ernestii Comber	SC: Kangding		16	2*x*	S. M. Mu & Shue (1985)
A. kialensis N. D. Simpson	YN		16	2*x*	S. M. Mu & Shue (1985)
A. pastorius Tsai & Yu	SC		32	4*x*	S. M. Mu & Shue (1985)
A. przewalskii Bunge ex Maxim.	SC		16	2*x*	S. M. Mu & Shue (1985)
A. strictus Graham	XZ: Bomi, 3300 m		32	4*x*	W. T. Wang et al. (1994)
A. tongolensis Ulbrich	SC		16	2*x*	S. M. Mu & Shue (1985)
Caragana bicolor Kom.	SC		16	2*x*	S. M. Mu & Shue (1985)
Crotalaria medicaginea Lam.	YN: Heqin		16	2*x*	J. Q. Li (1988)
C. sessiliflora L.	XZ: Motuo, 900 m		16	2*x*	Gu & Sun (1998)
Desmodium yunnanense Franch.	YN: Heqing		22	2*x*	Cui (1987)
Gueldenstaedtia delavayi Franch.	YN: Lijiang		16	2*x*	Nie (2002)
Mastersia assamica Benth.	XZ: Motuo, 900 m		22	2*x*	Gu & Sun (1998)
Medicago lupulina L.	SC: Baoxing	8		2*x*	Hong (1984)
Salweenia wardii Baker f.	SC: Daocheng		16	2*x*	Q. X. Zhou et al. (2000b)
Tibetia coelestis (Diels) H. P. Tsui	YN: Zhongdian		16	2*x*	Nie (2002)

Appendix 1. Continued.

Taxon	Locality	*n*	2*n*	Ploidy	Reference
T. himalaica (Baker) H. P. Tsui	SC: Daocheng		16	2*x*	Nie et al. (2002)
	SC: Litang		16	2*x*	Nie (2002)
T. tongolensis (Ulbr.) H. P. Tsui	SC: Daocheng		16	2*x*	Nie et al. (2002)
T. yunnanensis (Franch.) H. P. Tsui	YN: Zhongdian		16	2*x*	Nie et al. (2002)
Vicia hirsuta (L.) Gray	SC: Baoxing	7		2*x*	Hong (1984)
V. sativa L.	SC: Baoxing	6		2*x*	Hong (1984)
V. villosa Roth	SC: Baoxing		12	2*x*	Hong (1984)
FAGACEAE					
Quercus guyavaefolia H. Lév.	YN: Lijiang		24	2*x*	M. Cao & Zhou (2000)
FUMARIACEAE					
Corydalis omeiana H. Tsaung	SC: Mt. Emei, 1700 m	8		2*x*	Hong & Zhang (1990)
GENTIANACEAE					
Comastoma arrectum (Franch.) Holub	YN: Deqin, 3900 m		18	2*x*	J. Q. Liu & Ho (2002)
C. beesianum (W. W. Sm.) Holub	YN: Lijiang, 2800 m		18	2*x*	J. Q. Liu & Ho (2002)
C. chiuchiense T. N. Ho & J. Q. Liu	QH: Maqin, 4450 m		20	2*x*	J. Q. Liu & Ho (2002)
C. pulmonarium (Turcz.) Toyokuni	QH: Maqin, 4000 m		18	2*x*	J. Q. Liu & Ho (2002)
C. traillianum (Forrest) Holub	YN: Zhongdian, 3382 m		18	2*x*	J. Q. Liu & Ho (2002)
Gentiana alsinoides Franch.	YN: Lijiang, 2950 m		20	2*x*	Küpfer & Yuan (1996)
G. altorum Harry Sm.	SC: Kangding, 3600 m		24	2*x*	J. Q. Liu et al. (2002a)
G. ampla Harry Sm.	YN: Lijiang, 3700 m		48	4*x*	Chen et al. (1997)
G. arethusae Burkill subsp. *delicatula* (C. Marquand) Halda	YN: Deqin, 3800 m		24	2*x*	J. Q. Liu et al. (2002a)
G. aristata Maxim.	GS: Luqu, 3450 m	7	14	2*x*	Küpfer & Yuan (1996)
	GS: Maqu, 3500 m		14	2*x*	Yuan & Küpfer (1997)
G. asterocalyx Diels	YN: Lijiang, 2900 m		20	2*x*	Küpfer & Yuan (1996)
G. caeruleogrisea T. N. Ho	QH: Maqin, 3500 m		16	2*x*	Ho et al. (2002b)
G. callistantha Diels & Gilg	GS: Luqu, 3500 m		26	2*x*	Yuan & Küpfer (1997)
G. cephalantha Franch.	YN: Lijiang, 3000 m		24	2*x*	J. Q. Liu et al. (2002a)
G. chinensis Kusnezow	SC: Mt. Emei, 3000 m		24	2*x*	Ho et al. (2002a)
G. crassicaulis Duthie ex Burkill	YN: Zhongdian, 3300 m		26	2*x*	Yuan et al. (1998)
G. crassula Harry Sm.	YN: Lijiang, 4300 m		20	2*x*	Yuan et al. (1998)
G. crassuloides Bureau & Franch.	YN: Deqin, 4100 m		40	4*x*	Yuan et al. (1998)
G. crenulatotruncata (C. Marquand) T. N. Ho	GS: Maqu, 4200 m		18	2*x*	Yuan & Küpfer (1997)
G. delavayi Franch.	YN: Lijiang, 2900 m		26	2*x*	Yuan & Küpfer (1997)
G. exigua Harry Sm.	YN: Lijiang, 2400 m		20	2*x*	Küpfer & Yuan (1996)
G. haynaldii Kanitz	YN: Zhongdian, 3400 m		20	2*x*	Yuan & Küpfer (1997)
	XZ: Dingqing, 4250 m		20	2*x*	Yuan et al. (1998)
	SC: Litang, 3800 m		18	2*x*	S. L. Chen et al. (1997)
G. heleonastes Harry Sm.	GS: Maqu, 3650 m		12	2*x*	Küpfer & Yuan (1996)
	GS: Maqu, 3650 m		12	2*x*	Yuan & Küpfer (1997)
	GS: Maqu, 3900 m		36	6*x*	Yuan et al. (1998)
G. heterostemon Harry Sm.	YN: Dali, 2100 m		20	2*x*	Küpfer & Yuan (1996)
G. hyalina T. N. Ho	QH: Maduo, 4300 m		12	2*x*	Yuan & Küpfer (1997)
G. intricata C. Marquand	YN: Lijiang, 3200 m		20	2*x*	Küpfer & Yuan (1996)
	YN: Lijiang, 2700 m		20	2*x*	Yuan & Küpfer (1997)
G. leucomelaena Maxim.	SC: Ruoergai, 4200 m		36	4*x*	Yuan et al. (1998)
G. lhassica Burkill	XZ: Dingqing, 4200 m		26	2*x*	Yuan et al. (1998)
G. mairei H. Lév.	YN: Lijiang, 3200 m		20	2*x*	Yuan et al. (1998)

Appendix 1. Continued.

Taxon	Locality	*n*	2*n*	Ploidy	Reference
G. microdonta Franch.	YN: Lijiang, 3700 m		24	2*x*	S. L. Chen et al. (1997)
	YN: Lijiang, 2900 m		24	2*x*	Ho et al. (2002a)
G. nubigena Edgew.	QH: Maqin, 4900 m		24	2*x*	Ho et al. (2002b)
G. panthaica Burkill	YN: Dali, 3200 m		20	2*x*	Yuan & Küpfer (1997)
G. praticola Franch.	YN: Dali, 2200 m		20	2*x*	Küpfer & Yuan (1996)
G. prattii Kusnezow	SC: Sungpan, 3700 m		20	2*x*	Yuan et al. (1998)
	GS: Luqu, 3500 m		18	2*x*	Küpfer & Yuan (1996)
G. pseudoaquatica Kusnezow	GS: Luqu, 3300 m		20	2*x*	Küpfer & Yuan (1996)
	GS: Maqu, 3800 m		20	2*x*	Yuan & Küpfer (1997)
	XZ: Dingqing, 4250 m		20	2*x*	Yuan et al. (1998)
G. pseudosquarrosa Harry Sm.	SC: Sungpan, 3400 m		20	2*x*	Yuan et al. (1998)
G. pudica Maxim.	GS: Maqu, 3700 m		20	2*x*	Yuan & Küpfer (1997)
G. serra Franch.	YN: Lijiang, 2400 m		34	2*x*	Ho et al. (2002b)
G. souliei Franch.	YN: Lijiang, 2400 m		46	2*x*	Ho et al. (2002b)
G. squarrosa Ledeb.	GS: Luqu, 3700 m		38	2*x*	Yuan et al. (1998)
G. stipitata Edgew. subsp. *tizuensis* (Franch.) T. N. Ho	SC: Litang, 3800 m		26	2*x*	S. L. Chen et al. (1997)
G. straminea Maxim.	GS: Maqu, 3500 m		52	4*x*	Yuan & Küpfer (1997)
G. subintricata T. N. Ho	YN: Lijiang, 2900 m		20	2*x*	Küpfer & Yuan (1996)
	YN: Zhongdian, 3200 m		20	2*x*	Yuan et al. (1998)
G. tibetica King ex Hook. f.	XZ: Changdu, 3650 m		52	4*x*	Yuan et al. (1998)
G. veitchiorum Hemsl.	SC: Litang, 3800 m		24	2*x*	S. L. Chen et al. (1997)
G. waltonii Burkill	XZ: Quxu, 3700 m		26	2*x*	Ho et al. (2002a)
G. wasenensis C. Marquand	SC: Baoxing, 3400 m		24	2*x*	Ho et al. (2002b)
G. yunnanensis Franch.	YN: Dali, 3700 m		24	2*x*	Yuan et al. (1998)
Gentianella gentianoides (Franch.) Harry Sm.	YN: Lijiang, 2900 m		22	2*x*	J. Q. Liu et al. (2002c)
G. azurea (Bunge) Holub	QH: Dari, 4200 m		22	2*x*	J. Q. Liu et al. (2002c)
Gentianopsis barbata (Froel.) Ma	YN: Lijiang		26	2*x*	Yuan & Küpfer (1993)
G. grandis (Harry Sm.) Ma	YN: Lijiang		52	4*x*	Yuan & Küpfer (1993)
G. lutea Ma	YN: Lijiang		26	2*x*	Yuan & Küpfer (1993)
Lomatogoniopsis alpina T. N. Ho & S. W. Liu	QH: Dari		12	2*x*	J. Q. Liu et al. (2002b)
Megacodon stylophorus (C. B. Clarke) Harry Sm.	YN: Deqin		28	4*x*	J. Q. Liu et al. (2002b)
Swertia franchetiana Harry Sm.	XZ: Changdu, 3800 m		20	2*x*	T. N. He et al. (1999)
S. tetraptera Maxim.	QH: Maqin, 3800 m		14	2*x*	T. N. He et al. (1999)
S. wolfgangiana Gruning	QH: Maduo, 3700 m		28	4*x*	T. N. He et al. (1999)
GERANIACEAE					
Geranium eriostemon Fisch. ex DC.	SC: Baoxing, 2500 m	14		2*x*	Hong & Zhang (1990)
GESNERIACEAE					
Ancylostemon aureus (Franch.) B. L. Burtt	YN: Binchuan		34	2*x*	Y. Z. Wang & Gu (1999)
Corallodiscus flabellatus (Craib) B. L. Burtt	YN: Zhongdian		40	4*x*	Y. X. Lu et al. (2002)
Loxostigma griffithii (Wight) C. B. Clarke	YN: Rujiang River		34	2*x*	P. Zhou (2003)
JUGLANDACEAE					
Juglans sigillata Dode	YN: Yangbi		32	2*x*	Y. L. Mu et al. (1990)
LAURACEAE					

Appendix 1. Continued.

Taxon	Locality	*n*	2*n*	Ploidy	Reference
Cinnamomum longipaniculatum (Gamble) N. Chao ex H. W. Li	SC: Dujiangyan		24	2*x*	C. B. Chen et al. (1998)
Lindera communis Hemsl.	SC: Dujiangyan		24	2*x*	C. B. Chen et al. (1998)
L. megaphylla Hemsl.	SC: Dujiangyan		24	2*x*	C. B. Chen et al. (1998)
L. pulcherrima (Nees) Benth. ex Hook. f.	SC: Dujiangyan		24	2*x*	C. B. Chen et al. (1998)
LILIACEAE					
Allium carolinianum Delar.	QH: Maduo, 4450 m		16	2*x*	Huang et al. (1996a)
A. chienchuanense J. M. Xu	YN: Jianchuan, 2800 m		22	2*x*	Huang et al. (1995)
A. cyathophorum E. Bureau & Franch.	YN: Zhongdian, 3250 m		16	2*x*	
	XZ: Zhayab, 3780 m		16	2*x*	L. Yang et al. (1998)
A. fasciculatum Rendle	SC: Xiangcheng, 2950 m		20	2*x*	Huang et al. (1995)
	SC: Xiangcheng, 2800 m		20	2*x*	Xu et al. (1998)
A. hookeri Thwaites	YN: Zhongdian, 3200 m		22	2*x*	Huang et al. (1995)
	YN: Dali, 2050 m		33	3*x*	Huang et al. (1995)
	YN: Dali, 2050 m		44	4*x*	Huang et al. (1995)
A. hookeri Thwaites var. *muliense* Airy Shaw	YN: Zhongdian, 3200 m		22	2*x*	Huang et al. (1996b)
A. macranthum Baker	YN: Zhongdian, 3250 m		28	4*x*	Huang et al. (1996b)
	YN: Zhongdian, 3250 m		14	2*x*	Huang et al. (1995)
	YN: Zhongdian, 3250 m		28	4*x*	Huang et al. (1995)
A. macrostemon Bunge	SC: Wenchuan, 1200 m		32	4*x*	S. M. Zhu & Xu (1999)
A. nanodes Airy Shaw	SC: Daocheng, 4500 m		16	2*x*	Jing et al. (1999)
A. omeiense Z. Y. Zhu	SC: Emei, 1400 m		22	2*x*	Huang et al. (1995)
A. ovalifolium Hand.-Mazz.	SC: Wenchuan, 2200 m		24	3*x*	Jing et al. (1999)
	YN: Zhongdian, 3600 m		16	2*x*	Jing et al. (1999)
A. prattii C. H. Wright	SC: Lixian, 3600 m		32	4*x*	Jing et al. (1999)
	SC: Litang, 4100 m		16	2*x*	Jing et al. (1999)
A. przewalskianum Regel	QH: Maqin, 3400 m		32	4*x*	Xue et al. (2000)
	QH: Nangqian, 3550 m		64	6*x*	Xue et al. (2000)
	XZ: Zhayab, 3780 m		32	4*x*	L. Yang et al. (1998)
A. trifurcatum (Wang & Tang) J. M. Xu	YN: Zhongdian, 3300 m		16	2*x*	Huang et al. (1995)
A. tuberosum Rottl. ex Spreng.	YN: Baoshan, 1500 m		24	3*x*	Huang et al. (1985)
	SC: Lixian, 1100 m		32	4*x*	L. Yang et al. (1998)
A. wallichii Kunth	YN: Binchuan, 2900 m		14	2*x*	Huang et al. (1995)
	YN: Binchuan 3200 m		14	2*x*	Huang et al. (1996c)
A. wallichii Kunth var. *platyphyllum* (Diels) J. M. Xu	YN: Zhongdian, 3300 m		14	2*x*	Huang et al. (1995)
Cardiocrinum giganteum Makino	SC: Mt. Emei		24	2*x*	Tang et al. (1984)
	YN: Gongshan, 2700 m		24	2*x*	Xie et al. (1992)

Appendix 1. Continued.

Taxon	Locality	*n*	2*n*	Ploidy	Reference
Clintonia udensis Trautv. & Mey.	SC: Mt. Emei, 2750 m		14	2*x*	S. F. Li & Chang (1996)
	YN: Lijiang, 3700 m		28	4*x*	S. F. Li & Chang (1996)
	YN: Yunlong, 3300 m		14	2*x*	L. Wang et al. (1993)
Disporopsis aspersa (Hua) Engl.	SC: Mt. Emei		40	2*x*	Gu et al. (1990)
D. fusco-picta Hance	YN: Tengchong		40	2*x*	Gu et al. (1990)
Disporum bodinieri (H. Lév. & Vaniot) F. T. Wang & T. Tang	XZ: Motuo, 1500 m		16	2*x*	Gu & Sun (1998)
D. cantoniense Merr.	YN: Lijiang, 2600 m		14	2*x*	Gu et al. (1993a)
	SC: Mt. Emei	8		2*x*	Tang et al. (1984)
Fritillaria cirrhosa D. Don	YN: Gongshan, 4100 m		24	2*x*	Xie et al. (1992)
Hemerocallis forrestii Diels	YN: Lijiang, 3200 m		22	2*x*	Xiong & Chen (1998)
	YN: Lijiang		22	2*x*	Xiong et al. (1997)
H. multiflora Stout	YN: Dali, 2500 m		33	3*x*	Xiong & Chen (1998)
H. plicata Stapf	YN: Dali, 2300 m		22	2*x*	Xiong & Chen (1998)
	YN: Dali, 2300 m		22	2*x*	Xiong et al. (1997)
Lilium bakerianum Coll. & Hemsl. var. *rubrum* Stearn	YN: Dali, 3200 m		24	2*x*	L. Wang et al. (1993)
L. brownii F. E. Brown ex Spae	YN: Lushui, 2000 m		24	2*x*	Xie et al. (1992)
L.davidii Duch.	YN: Gongshan		36	3*x*	Xie & Wu (1993)
	YN: Dali, 2400 m		24	2*x*	Yu et al. (1996a)
L. duchartrei Franch.	YN: Zhongdian, 3200 m		24	2*x*	Huang & Li (1996)
L. henrici Franch.	YN: Lijiang, 2800 m		24	2*x*	L. Wang et al. (1993)
L. nepalense D. Don	YN: Lushui, 2700 m		24	2*x*	Xie et al. (1992)
L. souliei (Franch.) Sealy	YN: Gongshan, 3500 m		24	2*x*	Xie et al. (1992)
L. taliense Franch.	YN: Gongshan, 2000 m		24	2*x*	Xie et al. (1992)
Nomocharis aperta W. W. Sm. & W. E. Evans	YN: Gongshan, 3300 m		24	2*x*	Xie et al. (1992)
N. basilissa Farrer ex W. E. Evans	YN: Gongshan, 3400 m		24	2*x*	Xie et al. (1992)
N. biluoensis S. Y. Liang	YN: Lijiang, 3000 m		24	2*x*	L. Wang et al. (1993)
N. farreri Cox	YN: Lushui, 3100 m		24	2*x*	Xie et al. (1992)
N. forrestii Balf. f.	YN: Zhongdian		24	2*x*	Yu & Huang (1994)
	YN: Zhongdian, 3800 m		24	2*x*	Yu et al. (1996d)
N. mairei H. Lév.	YN: Dali, 3500 m		24	2*x*	Yu et al. (1996b)
N. meleagrina Franch.	YN: Gongshan, 3300 m		24	2*x*	Xie et al. (1992)
N. pardanthina Franch.	YN: Dali, 3200 m		24	2*x*	L. Wang et al. (1993)
	YN: Gongshan, 3000 m		24	2*x*	Xie et al. (1992)
N. pardanthina Franch. f. *punctulata* Sealy	YN: Gongshan, 3300 m		24	2*x*	Xie et al. (1992)
N. saluenensis Balf. f.	YN: Yunlong, 3100 m		24	2*x*	L. Wang et al. (1993)
Notholirion bulbiliferum (Lingelsh.) Stearn	YN: Zhongdian, 3400 m		24	2*x*	Yu et al. (1996c)
N. campanulatum Cotton & Stearn	YN: Dali, 3200 m		24	2*x*	L. Wang et al. (1993)
	YN: Ninglang, 3500 m		24	2*x*	Yu et al. (1996c)
Ophiopogon angustifoliatus (Wang & Tang) S. C. Chen	YN: Weixi, 3100 m		72	4*x*	D. M. Zhang (1998)
O. bodinieri H. Lév.	YN: Zhongdian, 3600 m		108	6*x*	D. M. Zhang (1998)

Appendix 1. Continued.

Taxon	Locality	*n*	2*n*	Ploidy	Reference
O. clarkei Hook. f.	YN: Lijiang, 2750 m		36	2*x*	D. M. Zhang (1998)
O. intermedius D. Don	YN: Lijiang, 2750 m		72	4*x*	D. M. Zhang (1998)
O. japonicus Ker Gawl.	YN: Weixi, 2500 m		108	6*x*	D. M. Zhang (1998)
Paris bashanensis F. T. Wang & T. Tang	YN: Dali		10	2*x*	Gu & Na (1986)
P. dulongensis H. Li & S. Kurita	YN: Gongshan, 1320 m		10	2*x*	Gu et al. (1992)
P. fargesii Franch.	SC: Mt. Emei	5		2*x*	Tang et al. (1984)
P. forrestii (Takht.) H. Li	YN: Tengchong		10	2*x*	Miyamoto et al. (1992)
	YN: Gongshan, 2350 m		10	2*x*	Gu et al. (1992)
	YN: Dali		10	2*x*	Gu & Na (1986)
P. mairei H. Lév.	YN: Dali		10	2*x*	Miyamoto et al. (1992)
	YN: Gongshan, 1700 m		10	2*x*	Gu et al. (1992)
	YN: Dali		10	2*x*	Gu & Na (1986)
P. marmorata Stearn	YN: Dali		10	2*x*	Gu & Na (1986)
P. polyphylla Sm.	SC: Wenchuan		10	2*x*	Hong & Zhu (1987)
	SC: Mt. Emei		20	4*x*	S. F. Wang & Xu (1989)
P. rugosa H. Li & S. Kurita	YN: Gongshan, 1500 m		10	2*x*	Gu et al. (1992)
P. thibetica Franch.	YN: Dali		10	2*x*	Miyamoto et al. (1992)
	YN: Dali		10	2*x*	Gu & Na (1986)
P. thibetica Franch. var. *apetala* Hand.-Mazz.	YN: Gongshan, 2300 m		10	2*x*	Gu et al. (1992)
Polygonatum alternicirrhosum Hand.-Mazz.	SC: Luding, 2800 m		32	2*x*	S. F. Chen (1989)
P. cathcartii Baker	YN: Gongshan, 2600 m		32	2*x*	L. Wang et al. (1993)
P. cirrhifolium Royle	XZ: Bomi, 3000 m		52	4*x*	Gu et al. (1993b)
	SC: Kangding, 3300 m		56	4*x*	S. F. Chen (1989)
	YN: Yunlong, 2900 m		30	2*x*	L. Wang et al. (1993)
P. curvistylum Hua	YN: Dali, 3000 m		78	6*x*	L. Wang et al. (1993)
P. griffithii Baker	XZ: Motuo, 1900 m		36	4*x*	Gu & Sun (1998)
P. odoratum Druce	SC: Mt. Emei, 800 m		22	2*x*	Fang (1989)
P. oppositifolium Royle	XZ: Motuo, 2100 m		30	2*x*	Gu & Sun (1998)
P. prattii Baker	YN: Dali		28	2*x*	J. Yang et al. (1992)
P. sibiricum Redouté	SC: Nanping, 3200 m		24	2*x*	S. F. Chen (1989)
Reineckea carnea (Andr.) Kunth	SC: Mt. Emei		38	2*x*	Tang et al. (1984)
Scilla sinensis (Lour.) Merr.	YN: Eryuan, Lijiang		16	2*x*	K. Y. Ding et al. (1998)
Smilacina atropurpurea (Franch.) Wang & Tang	YN: Yunlong, 2800 m		36	2*x*	L. Wang et al. (1993)
	YN: Zhongdian, 3800 m		72	4*x*	Meng et al. (2005)
S. forrestii (W. W. Sm.) Hand.-Mazz.	YN: Lushui, 3100 m		36	2*x*	Meng et al. (2005)
S. fusca Wall.	XZ: Motuo, 1600 m		54	3*x*	Gu & Sun (1998)
	YN: Yunlong, 2800 m		36	2*x*	L. Wang et al. (1993)
	YN: Gongshan, 1300 m		72	4*x*	Gu et al. (1992)
S. henryi (Baker) Hara	YN: Dali, 3200 m		36	2*x*	L. Wang et al. (1993)
S. lichiangense (W. W. Sm.) W. W. Sm.	YN: Zhongdian, 3700 m		36	2*x*	Meng et al. (2005)
S. purpurea Wall.	YN: Gongshan, 3300 m		36	2*x*	Meng et al. (2005)
S. tatsienensis (Franch.) Wehrh.	YN: Dali, 3200 m		36	2*x*	L. Wang et al. (1993)

Appendix 1. Continued.

Taxon	Locality	*n*	2*n*	Ploidy	Reference
Streptopus simplex D. Don	XZ: Motuo, 1700 m		32	4*x*	Gu & Sun (1998)
Trillium tschonoskii Maxim.	SC: Mt. Emei		10	2*x*	S. F. Wang (1989)
	SC: Mt. Emei		20	4*x*	S. F. Wang & Xu (1989)
ONAGRACEAE					
Circaea alpina L. subsp. *angustifolia* (Hand.-Mazz.) D. E. Boufford	YN: Hengduan Mts.		22	2*x*	Seavey & Boufford (1983)
ORCHIDACEAE					
Cymbidium hookerianum Rchb. f.	YN: Tengchong		40		Y. G. Li et al. (2003)
C. eburneum Lindl.	YN: Baoshan		40		Y. G. Li et al. (2003)
PAEONIACEAE					
Paeonia delavayi Franch.	YN: Lijiang, 2400 m		10	2*x*	D. Q. Yang & Zhu (1989)
P. delavayi Franch. f. *lutea* (Delavay ex Franch.) S. G. Haw	YN: Dali, 2910 m		10	2*x*	Gong et al. (1999)
	YN: Zhongdian, 3200 m		10	2*x*	Gong et al. (1991)
	YN: Dali, 3000 m		10	2*x*	D. Q. Yang & Zhu (1989)
P. obovata Maxim.	SC: Wolong Nat. Res.		20	4*x*	Hong et al. (2001)
PAPAVERACEAE					
Meconopsis integrifolia Franch.	YN: Zhangdian, 4150 m		76	4*x*	Meng et al. (in prep.)
M. horridula Hook. f. & Thomson	YN: Weixi, 4100 m		56	4*x*	Meng et al. (in prep.)
M. racemosa Maxim.	YN: Zhongdian, 4100 m		56	4*x*	Meng et al. (in prep.)
M. pseudovenusta G. Taylor	YN: Zhongdian, 4400 m		56	4*x*	Meng et al. (in prep.)
PLANTAGINACEAE					
Plantago erosa Wall.	SC: Baoxing, 1850 m	12		4*x*	Hong & Zhang (1990)
POACEAE					
Elymus anthosachnoides (Keng) Á. Löve	SC: Batang		28	4*x*	W. J. Li et al. (1996)
E. atratus (Nevski) Hand.-Mazz.	SC: Hongyuan		42	6*x*	Y. H. Liu (1985)
	SC: Rourgai		28	4*x*	B. R. Lu et al. (1990)
E. cylindricus Honda	SC: Ganzi		42	6*x*	Y. H. Liu (1985)
	SC: Hongyuan		42	6*x*	B. R. Lu et al. (1990)
E. dahuricus Turcz.	SC: Kangding		42	6*x*	Y. H. Liu (1985)
E. nutans Griseb.	SC: Ruoergai		42	6*x*	Y. H. Liu (1985)
E. sibiricus L.	SC: Kangding		28	4*x*	Y. H. Liu (1985)
	SC: Rourgai		28	4*x*	B. R. Lu et al. (1990)
	SC: Nanping		42	6*x*	B. R. Lu et al. (1990)
E. submuticus Keng ex Keng f.	SC		42	6*x*	L. B. Cai & Feng (1997)
E. tangutorum (Nevski) Hand.-Mazz.	SC: Shiqu		42	6*x*	Y. H. Liu (1985)
	SC: Maowen		42	6*x*	B. R. Lu et al. (1990)
Kengyilia laxiflora (Keng) S. L. Chen	SC: Ganzi		42	6*x*	X. Q. Zhang et al. (1998)
K. melanthera (Keng) S. L. Chen	SC: Ruoergai		42	6*x*	Y. H. Zhou (1994)
Poa attenuata Trin. ex Bunge var. *vivipara* Rendl	QH: BayanHarashan, 5200 m		ca. 21	3*x*	Huang et al. (1996a)
Roegneria altissima Keng ex Y. L. Keng & S. L. Chen	SC: Batang		28	4*x*	Y. H. Zhou et al. (1993)

Appendix 1. Continued.

Taxon	Locality	*n*	2*n*	Ploidy	Reference
R. breviglumis Keng ex Y. L. Keng & S. L. Chen	SC: Ruoergai		28	4*x*	B. R. Lu et al. (1990)
R. ciliaris (Trin.) Nevski	SC: Wenchuan		28	4*x*	B. R. Lu et al. (1990)
	SC: Yaan		28	4*x*	G. L. Sun et al. (1993b)
	SC: Nanping		14	2*x*	G. L. Sun et al. (1992)
R. dolichathera Keng ex Y. L. Keng & S. L. Chen	SC: Wenchuan		28	4*x*	Y. H. Zhou et al. (1993)
R. elytrigioides C. Yen & J. L. Yang	XZ: Chuangdu		28	4*x*	C. B. Ding et al. (2004)
R. gmelini (Griseb.) Kitag.	SC: Ruoergai		28	4*x*	B. R. Lu et al. (1990)
R. kamoji (Ohwi) Ohwi	SC: Lixian		42	6*x*	B. R. Lu et al. (1990)
	SC: Yaan		42	6*x*	X. Q. Zhang et al. (1998)
R. nutans (Keng) Keng ex Y. L. Keng & S. L. Chen	SC: Ruoergai		42	6*x*	B. R. Lu et al. (1990)
	SC: Hongyuan		28	4*x*	G. L. Sun et al. (1993a)
	SC: Hongyuan		42	6*x*	B. R. Lu et al. (1990)
R. parvigluma Keng ex Y. L. Keng & S. L. Chen	SC: Maerkang		28	4*x*	B. R. Lu et al. (1990)
	SC: Lixian		42	6*x*	B. R. Lu et al. (1990)
R. pendulina Nevski	SC: Lixian		28	4*x*	B. R. Lu et al. (1990)
	SC: Nanping		28	4*x*	B. R. Lu et al. (1990)
R. sinica Keng ex Y. L. Chen & S. L. Chen	SC: Aba		28	4*x*	B. R. Lu et al. (1990)
R. stricta Keng ex Y. L. Keng & S. L. Chen	SC: Maowen		28	4*x*	B. R. Lu et al. (1990)
PRIMULACEAE					
Androsace bulleyana Forrest	YN: Zhongdian, 3400 m		20	2*x*	Nakata et al. (1997)
A. spinulifera Knuth	YN: Lijiang, 3200 m		20	2*x*	Nakata et al. (1997)
A. yargongensis Petitm.	QH: Maduo, 4600 m		40	4*x*	Huang (2001)
Pomatosace filicula Maxim.	QH: Maqin		20	2*x*	Kong & Liu (1999)
Primula aurantiaca W. W. Sm.	YN: Jianchuan, 3100 m		22	2*x*	H. F. Zhu et al. (2001)
P. beesiana Forrest	YN: Lijiang, 2800 m		22	2*x*	H. F. Zhu et al. (2001)
	YN: Lijiang, 2500 m		22	2*x*	Nakata et al. (1997)
P. bulleyana Forrest	YN: Lijiang, 2800 m		22	2*x*	H. F. Zhu et al. (2001)
P. forrestii Balf. f.	YN: Lijiang, 2700 m		24	2*x*	Nakata et al. (1997)
P. malacoides Franch.	YN: Zhongdian, 3200 m		18	2*x*	Nakata et al. (1997)
P. monticola (Hand.-Mazz.) F. H. Chen & C. M. Hu	SC: Wenchuan, 3700 m		16	2*x*	H. F. Zhu et al. (2001)
P. poissonii Franch.	YN: Zhongdian, 3300 m		22	2*x*	H. F. Zhu et al. (2001)
	YN: Zhongdian, 3300 m		22	2*x*	Nakata et al. (1997)
P. pulchella Franch.	YN: Lijiang, 2800 m		16	2*x*	Nakata et al. (1997)
P. pulverulenta Duthie	SC: Kangdian, 2500 m		22	2*x*	H. F. Zhu et al. (2001)
P. secundiflora Franch.	YN: Deqin, 4300 m		22	2*x*	H. F. Zhu et al. (2001)
	YN: Zhongdian, 3100 m		22	2*x*	Nakata et al. (1997)
P. sikkimensis Hook.	YN: Deqin, 4300 m		20	2*x*	H. F. Zhu et al. (2001)
P. sinolisteri Balf. f.	YN: Luquan, 2500 m		24	2*x*	Nakata et al. (1997)
	YN: Zhongdian, 3100 m		22	2*x*	Nakata et al. (1997)

Appendix 1. Continued.

Taxon	Locality	*n*	2*n*	Ploidy	Reference
P. vialii Delavay ex Franch.	YN: Zhongdian, 4050 m		22	2*x*	H. F. Zhu et al. (2001)
RANUNCULACEAE					
Aconitum brachypodum Diels	YN: Lijiang, 3700 m		16	2*x*	Q. E. Yang et al. (1993a)
A. brachypodium Diels var. *laxiflorum* H. R. Fletcher & Lauener	YN: Zhongdian, 3200 m		16	2*x*	Q. E. Yang et al. (1993a)
A. brevicalcaratum Diels	YN: Heqing, 3700 m		32	4*x*	Q. E. Yang et al. (1994)
	YN: Lijiang		32	4*x*	Q. E. Yang et al. (1989)
A. brevicalcaratum (Finet & Gagnep.) Diels var. *parviflorum* Chen & Liu	YN: Lijiang, 4000 m		32	4*x*	Q. E. Yang et al. (1994)
A. brunneum Hand.-Mazz.	SC: Songpan		16	2*x*	Q. E. Yang (1996)
A. bulleyanum Diels	YN: Heqing		16	2*x*	Q. E. Yang et al. (1989)
A. carmichaelii Debeaux	YN: Dali		64	8*x*	Q. E. Yang et al. (1989)
A. contortum Finet & Gagnep.	YN: Yunlong, 3400 m		16	2*x*	Q. E. Yang et al. (1993a)
	YN: Dali		16	2*x*	Q. E. Yang et al. (1989)
A. crassiflorum Hand.-Mazz.	YN: Zhongdian, 3700 m		32	4*x*	Q. E. Yang et al. (1994)
	SC: Yajiang		32	4*x*	Q. E. Yang (2001a)
A. delavayi Franch.	YN: Lijiang, 2900 m		16	2*x*	Q. E. Yang et al. (1993a)
	YN: Dali		16	2*x*	Q. E. Yang (2001a)
A. episcopale H. Lév.	YN: Dali		16	2*x*	Q. E. Yang et al. (1989)
A. fengii W. T. Wang	YN: Zhongdian, 3700 m		32	4*x*	Q. E. Yang et al. (1993a)
	YN: Zhongdian, 3970 m		16	2*x*	Q. E. Yang et al. (1993a)
	YN: Weixi		16	2*x*	Q. E. Yang (2001a)
A. forrestii Stapf	YN: Lijiang		16	2*x*	Q. E. Yang et al. (1989)
A. georgei Comber	YN: Lijiang, 3200 m		16	2*x*	Q. E. Yang et al. (1993a)
A. gymnandrum Maxim.	QH: Dari, 4050 m		16	2*x*	J. Q. Liu (2002)
A. hemsleyanum E. Pritz. ex Diels	YN: Deqin, 3200 m		16	2*x*	Q. E. Yang et al. (1993a)
	YN: Weixi		16	2*x*	Q. E. Yang (2001a)
A. hemsleyanum E. Pritz. var. *circinatum* W. T. Wang	SC: Mt. Emei, 2100 m		16	2*x*	Shang & Li (1984)
A. legendrei Hand.-Mazz.	SC: Shimian		16	2*x*	Q. E. Yang (2001a)
A. liljestrandii Hand.-Mazz.	SC: Yajiang		16	2*x*	Q. E. Yang (2001a)
A. nagarum Stapf	YN: Yunlong		16	2*x*	Q. E. Yang et al. (1993a)
A. nagarum Stapf var. *heterotrichum* H. R. Fletcher & Lauener	YN: Weixi, 3600 m		16	2*x*	Q. E. Yang et al. (1993a)
A. nagarum Stapf var. *dielsianum* (Airy Shaw) W. T. Wang	YN: Tengchong		16	2*x*	Q. E. Yang et al. (1989)
A. ouvrardianum Hand.-Mazz.	YN: Deqin, 3600–4000 m		16	2*x*	Q. E. Yang et al. (1993a)
	YN: Deqin, 4200 m		16	2*x*	Q. E. Yang et al. (1993a)

Appendix 1. Continued.

Taxon	Locality	*n*	2*n*	Ploidy	Reference
A. pendulicarpum Chang ex W. T. Wang	YN: Deqin		16	2*x*	Q. E. Yang et al. (1989)
A. pendulum Busch	YN: Zhongdian, 3200 m		16	2*x*	Q. E. Yang et al. (1993a)
A. piepunense Hand.-Mazz.	YN: Zhongdian, 3200 m		32	4*x*	Q. E. Yang et al. (1993a)
	YN: Zhongdian, 3400 m		16	2*x*	Q. E. Yang et al. (1993a)
	YN: Zhongdian	16		2*x*	Q. E. Yang (2001a)
A. piepunense Hand.-Mazz. var. *pilosum* H. F. Comber	YN: Zhongdian, 3700 m	16		2*x*	Q. E. Yang et al. (1993a)
A. pulchellum Hand.-Mazz.	YN: Deqin, 4200 m	16		2*x*	Q. E. Yang et al. (1993a)
A. rockii Fletcher & Lauener	YN: Zhongdian, 3750 m	16		2*x*	Q. E. Yang et al. (1993a)
	YN: Zhongdian, 3970 m	32		4*x*	Q. E. Yang et al. (1993a)
A. scaposum Franch.	YN: Dali	16		2*x*	Q. E. Yang (2001a)
A. sessiliflorum (Finet & Gagnep.) Hand.-Mazz.	SC: Ruoergai	16		2*x*	Q. E. Yang (1996)
A. sinomontanum Nakai	SC: Nanping	16		2*x*	Q. E. Yang (1996)
A. souliei Finet & Gagnep.	YN: Deqin, 4300 m	16		2*x*	Q. E. Yang et al. (1993a)
A. spathulatum W. T. Wang	YN: Heqing,	16		2*x*	Q. E. Yang et al. (1989)
A. stapfianum Hand.-Mazz.	YN: Lijiang	16		2*x*	Q. E. Yang et al. (1989)
A. stramineiflorum Chang ex W. T. Wang	YN: Weixi	16		2*x*	Q. E. Yang et al. (1993a)
A. tanguticum (Maxim.) Stapf	QH: Yushu, 3500 m	16		2*x*	J. Q. Liu (2002)
A. tongolense Ulbr.	SC: Lixian	16		2*x*	Q. E. Yang (2001a)
A. transsectum Diels	YN: Lijiang, 3600 m	16		2*x*	Q. E. Yang et al. (1993a)
	YN: Lijiang, Yulong	16		2*x*	Q. E. Yang et al. (1989)
A. tsaii W. T. Wang	YN: Lushui, 3200–3800 m	16		2*x*	Q. E. Yang et al. (1993a)
A. tuguancunense Q. E. Yang	YN: Zhongdian, 2800 m	16		2*x*	Q. E. Yang et al. (1993a)
	YN: Zhongdian	16		2*x*	Q. E. Yang & Gong (1995)
A. wangii Q. E. Yang	YN: Lijiang, 3200 m	16		2*x*	Q. E. Yang et al. (1993a)
A. wardii Fletcher & Lauener	YN: Deqin	32		4*x*	Q. E. Yang et al. (1994)
Actaea asiatica Hara	YN: Dali	16		2*x*	Q. E. Yang (1998)
	YN: Zhongdian	16		2*x*	Q. E. Yang (2002a)
Adonis brevistyla Franch.	YN: Zhongdian	16		2*x*	Q. E. Yang (2001b)
Anemoclema glaucifolium (Franch.) W. T. Wang	YN: Lijiang	16		2*x*	Q. E. Yang (2002b)
	YN: Ninglang	16		2*x*	G. L. Zhang & Gong (2002)
Anemone davidii Franch.	YN: Weixi	32		4*x*	Q. E. Yang (2002b)
A. begoniifolia H. Lév. & Vaniot	SC: Nanchuan	16		2*x*	Q. E. Yang (2002b)
A. demissa Hook. f. & Thomson	YN: Zhongdian	14		2*x*	Q. E. Yang (2002b)
A. flaccida Fr. Schmidt	YN: Weixi	14		2*x*	Q. E. Yang (2002b)

Appendix 1. Continued.

Taxon	Locality	*n*	2*n*	Ploidy	Reference
A. hupehensis Hort. ex Boynton f. *alba* W. T. Wang	YN: Zhongdian		16	2*x*	Q. E. Yang (2002b)
A. rivularis Wall.	YN: Lijiang		16	2*x*	Q. E. Yang (2002b)
A. rupestris Wall.	YN: Zhongdian		14	2*x*	Q. E. Yang (2002b)
A. stolonifera Maxim.	YN: Zhongdian		16	2*x*	Q. E. Yang (2002b)
A. trullifolia Hook. f. & Thomson var. *colestina* (Franch.) Finet & Gagnep.	YN: Dali		14	2*x*	Q. E. Yang (2002b)
A. trullifolia Hook. f. & Thomson var. *holophylla* Diels	YN: Zhongdian		14	2*x*	Q. E. Yang (2002b)
Asteropyrum peltatum J. R. Drumm. & Hutchinson	YN: Gongshan		16	2*x*	Q. E. Yang et al. (1993b)
	SC: Mt. Emei, 2000 m		16	2*x*	Z. Y. Zhang (1982)
Batrachium bungei (Steud.) L. Liu	YN: Zhongdian		24	3*x*	Q. E. Yang (2001b)
	YN: Zhongdian		16	2*x*	Q. E. Yang (2001b)
Beesia calthifolia Ulbr.	SC: Mt. Emei		16	2*x*	Shang (1985)
	YN: Dali		32	4*x*	Q. E. Yang (1999a)
	YN: Weixi		16	2*x*	Q. E. Yang (2002a)
B. deltophylla C. Y. Wu	XZ: Motuo		16	2*x*	Q. E. Yang et al. (1995)
Calathodes oxycarpa Sprague	YN: Dali, 2800 m		16	2*x*	Q. E. Yang (1995)
	SC: Mt. Emei, 2400 m		16	2*x*	Z. Y. Zhang (1982)
	YN: Dali		16	2*x*	Q. E. Yang (2002a)
Callianthemum pimpinelloides (D. Don) Hook. f. & Thomson	YN: Zhongdian		32	4*x*	Q. E. Yang (2001b)
Caltha palustris L.	YN: Dali		32	4*x*	Q. E. Yang (2002a)
	YN: Zhongdian		48	6*x*	Q. E. Yang (2002a)
	YN: Deqin		64	8*x*	Q. E. Yang (2002a)
Cimicifuga foetida L.	YN: Zhongdian		16	2*x*	Q. E. Yang (1999b)
	YN: Dali		32	4*x*	Q. E. Yang (1999b)
	YN: Zhongdian		16	2*x*	Q. E. Yang et al. (1993b)
C. foetida L. var. *velutina* Franch. ex Finet & Gagnep.	YN: Lijiang		16	2*x*	Q. E. Yang (1999b)
C. simplex Wormsk. ex DC.	SC: Muli		16	2*x*	Q. E. Yang (1999b)
C. yunnanensis Hsiao	YN: Lijiang		16	2*x*	Q. E. Yang (1999b)
	YN: Deqin		16	2*x*	Q. E. Yang (2002a)
Circaeaster agrestis Maxim.	QH: Datong		30	2*x*	Kong & Yang (1997)
Clematis brevicaudata DC.	YN: Deqin		16	2*x*	Q. E. Yang (2002b)
C. chrysocoma Franch.	YN: Lijiang		16	2*x*	Q. E. Yang (2002b)
C. kockiana C. K. Schneid.	YN: Yunlong		16	2*x*	Q. E. Yang (2002b)
C. puberula Hook. f. & Thomson var. *ganpiniana* (H. Lév. & Vaniot) W. T. Wang	YN: Lijiang		16	2*x*	Q. E. Yang (2002b)
C. ranunculoides Franch.	YN: Zhongdian		16	2*x*	Q. E. Yang (2002b)
C. rehderiana Craib	YN: Deqin		16	2*x*	Q. E. Yang (2002b)
Coptis teeta Wall.	YN: Gongshan		18	2*x*	Q. E. Yang et al. (1993b)
Delphinium beesianum W. W. Sm.	YN: Zhongdian		16	2*x*	Q. E. Yang (2001a)
D. bonvalotii Franch.	SC: Muli		16	2*x*	Q. E. Yang (2001a)
D. bulleyanum Forrest ex Diels	YN: Zhongdian		16	2*x*	Q. E. Yang (2001a)
D. caeruleum Jacquem.	SC: Ruoergai		16	2*x*	Q. E. Yang (1996)
D. candelabrum Ostenf. var. *monanthum* (Hand.-Mazz.) W. T. Wang	QH: Yushu, 4650 m		16	2*x*	J. Q. Liu & He (1999)
D. ceratophorum Franch.	YN: Weixi		16	2*x*	Q. E. Yang (2001a)
D. coleopodum Hand.-Mazz.	YN: Lijiang		16	2*x*	Q. E. Yang (2001a)
D. delavayi Franch.	YN: Lijiang		16	2*x*	Q. E. Yang (2001a)

Appendix 1. Continued.

Taxon	Locality	*n*	2*n*	Ploidy	Reference
D. delavayi Franch. var. *pogonanthum* (Hand.-Mazz.) W. T. Wang	YN: Zhongdian		16	2*x*	Q. E. Yang (2001a)
D. forrestii Diels	YN: Zhongdian		16	2*x*	Q. E. Yang (2001a)
D. grandiflorum L.	SC: Lixian		16	2*x*	Q. E. Yang (2001a)
D. kamaonense Huth	SC: Nanping		16	2*x*	Q. E. Yang (1996)
D. kamaonense var. *glabrescens* (W. T. Wang) W. T. Wang	QH: Yushu, 4020 m		16	2*x*	J. Q. Liu & He (1999)
D. likiangense Franch.	YN: Zhongdian		16	2*x*	Q. E. Yang (2001a)
D. nangchienense W. T. Wang	QH: Yushu, 3540 m		16	2*x*	J. Q. Liu & He (1999)
D. oxycentrum W. T. Wang	YN: Zhongdian		16	2*x*	Q. E. Yang (2001a)
D. pylzowi Maxim.	QH: Yushu, 4000 m		16	2*x*	J. Q. Liu & He (1999)
D. smithianum Hand.-Mazz.	YN: Zhongdian		16	2*x*	Q. E. Yang (2001a)
D. spirocentrum Hand.-Mazz.	YN: Dali		16	2*x*	Q. E. Yang (2001a)
D. tangkulaense W. T. Wang	QH: Maduo, 4430 m		16	2*x*	J. Q. Liu & He (1999)
D. tenii H. Lév.	YN: Zhongdian		16	2*x*	Q. E. Yang (2001a)
D. trichophorum Franch.	QH: Yushu, 3850 m		16	2*x*	Liu & He (1999)
D. umbrosum Hand.-Mazz.	YN: Weixi		16	2*x*	Q. E. Yang (2001a)
Halerpestes sarmentosa (Adams) Komarov	YN: Zhongdian		32	4*x*	Q. E. Yang (2001b)
Kingdonia uniflora Balf. f. & W. W. Sm.	SC: Mt. Emei, 2750 m		18	2*x*	Z. Y. Zhang (1982)
Oxygraphis delavayi Franch.	YN: Weixi, 3900 m		16	2*x*	Q. E. Yang (2000a)
O. glacialis Bunge	YN: Deqin, 3900 m		16	2*x*	Q. E. Yang (2000a)
O. tenuifolia W. E. Evans	YN: Zhongdian, 4100 m		16	2*x*	Q. E. Yang (2000a)
Ranunculus felixii H. Lév.	YN: Lijiang, 3600 m		32	4*x*	Q. E. Yang (2000b)
R. ficariifolia H. Lév. & Vaniot	YN: Weixi		32	4*x*	Q. E. Yang (2001b)
R. involucratus Maxim.	QH: Maduo, 4840 m		ca. 42	6*x*	Huang et al. (1996a)
R. japonicus Thunb.	SC: Yaan		14	2*x*	Q. E. Yang (2001b)
R. laetus Wall.	YN: Dali		14	2*x*	Q. E. Yang (2001b)
R. nematolobus Hand.-Mazz.	YN: Dali		16	2*x*	Q. E. Yang (2001b)
R. potanini Komarov	YN: Zhongdian		32	4*x*	Q. E. Yang (2001b)
R. sinovaginatus W. T. Wang	YN: Deqin		32	4*x*	Q. E. Yang (2001b)
R. tanguticus (Finet & Gagnep.) Hao	SC: Lixian		32	4*x*	Q. E. Yang (2001b)
R. trigonus Hand.-Mazz.	YN: Lijiang		16	2*x*	Q. E. Yang (2001b)
R. wangianus Q. E. Yang	YN: Weixi		48	6*x*	Q. E. Yang (2000b)
R. yunnanensis Franch.	YN: Dali, 3400 m		16	2*x*	Q. E. Yang (2000b)
Souliea vaginata Franch.	YN: Zhongdian		16	2*x*	Q. E. Yang (2002a)
Trollius yunnanensis Ulbr.	YN: Lijiang		16	2*x*	Q. E. Yang (2002a)
ROSACEAE					
Dichotomanthes tristaniaecarpa Kurz	YN: Tengchong		34	2*x*	L. H. Zhou et al. (2000)
Malus asiatica Nakai	SC: Baxian		68	4*x*	G. L. Liang (1987)
M. halliana Koehne	SC: Zhaojiao		34	2*x*	G. L. Liang (1987)
	SC: Zhaojiao		34	2*x*	G. L. Liang & Li (1993)
M. hupehensis (Pamp.) Rehder	SC: Maerkang		51	3*x*	G. L. Liang (1987)
	SC: Yanyuan		68	4*x*	G. L. Liang (1987)
M. kansuensis (Batalin) C. K. Schneid.	SC: Xiaojin		34	2*x*	G. L. Liang (1987)
M. ombrophila Hand.-Mazz.	SC: Yanyuan		34	2*x*	G. L. Liang (1987)
	SC: Yanyuan		34	2*x*	G. L. Liang & Li (1993)

Appendix 1. Continued.

Taxon	Locality	*n*	2*n*	Ploidy	Reference
M. rockii Rehder	SC: Yanyuan		34	2*x*	G. L. Liang (1987)
	SC: Zhaojiao		51	3*x*	G. L. Liang (1987)
	SC: Zhaojiao		51	3*x*	G. L. Liang & Li (1993)
	SC: Yanyuan		34	2*x*	G. L. Liang & Li (1993)
M. sikkimensis (Wenzig) Koehne ex C. K. Schneid.	SC: Yanyuan		34	2*x*	G. L. Liang & Li (1993)
M. toringoides (Rehd.) Hughes	SC: Maerkang		51	3*x*	G. L. Liang (1987)
	SC: Aba		34	2*x*	G. L. Liang & Li (1993)
	SC: Maerkang		51	3*x*	G. L. Liang & Li (1993)
	SC: Aba		68	4*x*	G. L. Liang & Li (1993)
M. xiaojinensis M. H. Cheng & N. G. Jiang	SC: Xiaojin		68	4*x*	G. L. Liang & Li (1993)
M. yunnanensis C. K. Schneid.	SC: Yanyuan		34	2*x*	G. L. Liang (1987)
	SC: Yanyuan		34	2*x*	G. L. Liang & Li (1993)
Rubus ichangensis Hemsl. & Kuntze	SC: Mt. Emei		28	4*x*	Iwatsubo & Naruhashi (1992)
RUBIACEAE					
Kelloggia chinensis Franch.	YN: Zhongdian		22	2*x*	Tu et al. (in prep.)
SABIACEAE					
Sabia yunnanensis Franch.	SC: Baoxing, 2600 m	12		2*x*	Hong & Zhang (1990)
SAXIFRAGACEAE					
Chrysosplenium griffithii Hook. f. & Thomson	SC: Kangding, 3560 m		18	2*x*	Funamoto et al. (1997b)
	SC: Songpan, 3400 m		36	4*x*	Funamoto et al. (2000b)
C. lanuginosum Hook. f. & Thomson	SC: Dujianyan, 1900 m		16	2*x*	Funamoto et al. (2000b)
C. aff. *lixianense* Jien ex J. T. Pan	SC: Nanping, 3050 m		12	2*x*	Funamoto et al. (2000b)
C. pillosum Maxim. var. *valdipilosum* Ohwi	SC: Songpan, 3400 m		36	4*x*	Funamoto et al. (2000b)
C. qinlingense Jien ex J. T. Pan	SC: Nanping, 3050 m		52	4*x*	Funamoto et al. (2000b)
Parnassia aff. *cacuminum* Hand.-Mazz. f. *yushuensis* T. C. Ku	SC: Songpan, 3850 m		18	2*x*	Funamoto et al. (2001a)
P. brevistyla (Brieg.) Hand.-Mazz.	SC: Songpan, 3420 m		14	2*x*	Funamoto et al. (2001a)
P. delavayi Franch.	SC: Nanping, 3050 m		14	2*x*	Funamoto et al. (2001a)
P. viridifolia Batalin	SC: Nanping, 3050 m		36	4*x*	Funamoto et al. (2001a)
P. yunnanensis Franch. var. *longistipitata* Z. P. Jien	SC: Kangdin, 3750 m		32	4*x*	Funamoto et al. (1997a)
Rodgersia aesculifolia Batalin	SC: Aba, Maoxian		30	2*x*	Funamoto et al. (2000a)
R. pinnata Franch.	YN: Lijiang		60	4*x*	Akiyama et al. (1990)
	YN: Lijiang		ca. 75	5*x*	Akiyama et al. (1990)
Saxifraga aculeate Balf. f.	SC: Kangdin, 2400 m		28	4*x*	Funamoto et al. (1998)

Appendix 1. Continued.

Taxon	Locality	*n*	2*n*	Ploidy	Reference
S. aurantiana Franch.			16	2*x*	Funamoto et al. (2001b)
S. cardiophylla Franch.	SC: Kangdin, 3620 m		32	4*x*	Funamoto et al. (1998)
S. divaricata Engl. & Irmscher	SC: Kangdin, 3750 m		22	2*x*	Funamoto et al. (1998)
S. egregia Engl.	SC: Songpan, 3500 m		16	2*x*	Funamoto et al. (2001b)
S. heleonastes Harry Sm.	SC: Songpan, 3350 m		16	2*x*	Funamoto et al. (2001b)
S. hirculus L.	SC: Songpan, 3850 m		32	4*x*	Funamoto et al. (2001b)
S. aff. *melanocentra* Franch.	SC: Songpan, 3850 m		22, 23	2*x*	Funamoto et al. (2001b)
S. montana Harry Sm.	SC: Kangdin, 3540 m		32	4*x*	Funamoto et al. (1998)
Tiarella polyphylla D. Don	SC: Mt. Emei		14	2*x*	Soltis & Bohm (1984)
SCROPHULARIACEAE					
Pedicularis densispica Franch. ex Maxim.	YN: Zhongdian		16	2*x*	J. Cai et al. (2004)
P. dichotoma Bonati	YN: Zhongdian		16	2*x*	J. Cai et al. (2004)
P. dolichocymba Hand.-Mazz.	YN: Zhongdian		16	2*x*	J. Cai et al. (2004)
P. integrifolia Hook. f. subsp. *integerrima* (Pennell & Li) Tsoong	YN: Zhongdian		14	2*x*	J. Cai et al. (2004)
P. longiflora Rudolph var. *tubiformis* (Klotzsch) Tsoong	YN: Zhongdian		16	2*x*	J. Cai et al. (2004)
P. oxycarpa Franch. ex Maxim.	YN: Zhongdian		16	2*x*	J. Cai et al. (2004)
P. rex C. B. Clarke ex Maxim.	YN: Zhongdian		16	2*x*	J. Cai et al. (2004)
P. siphonantha D. Don var. *delavayi* (Franch. ex Maxim.) Tsoong	YN: Zhongdian		14	2*x*	J. Cai et al. (2004)
P. strobilacea Franch. ex Hemsl.	YN: Zhongdian		16	2*x*	J. Cai et al. (2004)
P. trichoglossa Hook. f.	YN: Deqin		16	2*x*	J. Cai et al. (2004)
P. tricolor Hand.-Mazz.	YN: Zhongdian		16	2*x*	J. Cai et al. (2004)
P. tsekouensis Bonati	YN: Zhongdian		16	2*x*	J. Cai et al. (2004)
P. umbelliformis Li	YN: Zhongdian		16	2*x*	J. Cai et al. (2004)
Veronica henryi T. Yamaz.	SC: Mt. Emei, 1700 m	16		4*x*	Hong & Zhang (1990)
V. javanica Blume	SC: Mt. Emei, 1000 m		16	2*x*	Hong & Zhang (1990)
V. laxa Benth.	SC: Baoxing, 1600 m		16	2*x*	Hong & Zhang (1990)
V. serpyllifolia L.	SC: Baoxing, 2500 m	7		2*x*	Hong & Zhang (1990)
SMILACACEAE					
Heterosmilax yunnanensis Gagnep.	SC: Mt. Emei, 1700 m		32	2*x*	Fu et al. (1995a, 1995b)
Smilax chapaensis Gagnep.	SC: Mt. Emei		32	2*x*	Fu et al. (1993)
	SC: Mt. Emei		32	2*x*	Fu et al. (1992)
S. menispermoidea A. DC.	SC: Mt. Emei		32	2*x*	Fu et al. (1995a, 1995b)
S. tsingchengshanensis Wang	SC: Mt. Emei, 1500 m		32	2*x*	Fu et al. (1993)
SOLANACEAE					
Anisodus acutangulus C. Y. Wu & C. Chen	YN: Lijiang, 3100 m		48	4*x*	Tu et al. (2005)
	SC: Daocheng, 3750 m		48	4*x*	Tu et al. (2005)
A. carniolicoides (C. Y. Wu & C. Chen) D'Arcy & Zhi Y. Zhang	YN: Zhongdian, 3370 m		48	4*x*	Tu et al. (2005)
A. luridus Link & Otto	YN: Heqing, 2390 m		48	4*x*	Tu et al. (2005)
A. sinensis Pascher	SC: Shizhu, 2900 m		48	4*x*	Tu et al. (2005)
A. tanguticus Pascher	SC: Daocheng, 3750 m		48	4*x*	Tu et al. (2005)
Hyoscyamus niger L.	SC: Ganzi, 3400 m		34	2*x*	Tu et al. (2005)

Appendix 1. Continued.

Taxon	Locality	*n*	2*n*	Ploidy	Reference
Mandragora caulescens C. B. Clarke	YN: Zhongdian, 3700 m		48	4*x*	Tu et al. (2005)
Przewalskia tangutica Maxim.	QH: Maduo, 4000 m		44	4*x*	Huang et al. (1996a)
	SC: Shiqu, 4320 m		44	4*x*	Tu et al. (2005)
Solanum spirale Roxb.	XZ: Motuo, 900 m		48	4*x*	Gu & Sun (1998)
THEACEAE					
Camellia pitardii Cohen Stuart	SC: Huili, 2150 m	15	30	2*x*	Gu (1997)
C. reticulata Lindl.	SC: Yanbian, 1650 m	30	60	4*x*	Gu (1997)
	SC: Miyi, 1850 m	45	90	6*x*	Gu (1997)
	YN: Tengchong		90	6*x*	Gu et al. (1988)
	YN: Tengchong	45		6*x*	T. J. Xiao et al. (1993)
	SC: Yanbian	15	30	2*x*	Xia et al. (1994)
	YN: Tengchong	45		6*x*	Gu et al. (1988)
	SC: Panzhihua, 1700 m	45		6*x*	Gu (1997)
	SC: Dukou, 2000 m		90	6*x*	T. J. Xiao et al. (1996)
	SC: Huili, 2650–2900 m		30	2*x*	T. J. Xiao et al. (1996)
	SC: Huili, 2650–2900 m		60	4*x*	T. J. Xiao et al. (1996)
	SC: Yanbian, 2600 m	15	30	2*x*	Gu (1997)
	YN: Huaping, 1900 m	45	90	6*x*	Gu (1997)
C. saluenensis Stapf ex Bean	YN: Baoshan	15		2*x*	T. J. Xiao et al. (1993)
	SC: Huili, 1650–1900 m	15	30	2*x*	Gu (1997)
VALERIANACEAE					
Valeriana hardwickii Wall. subsp. *latifolia* (Rehd. & Wils.) Y. F. Wu	SC: Mt. Emei, 1600 m	8		2*x*	Hong & Zhang (1990)
VELLOZIACEAE					
Acanthochlamys bracteata P. C. Kao	SC: Daofu, 2700–3400 m		38	2*x*	Kao et al. (1993)
ZINGIBERACEAE					
Caulokaempferia yunnanensis (Gagnep.) R. M. Sm.	SC: Dukou		42	2*x*	Z. Y. Chen et al. (1988)
Globba emeiensis Z. Y. Zhu	SC: Mt. Emei		24	2*x*	Z. Y. Chen et al. (1988)
Roscoea tibetica Batalin	YN: Lijiang		24	2*x*	Z. Y. Chen et al. (1988)

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CONTENTS

African Plant Diversity and Climate Change — *Colin J. McClean, Jon C. Lovett, Wolfgang Küper, Lee Hannah, Jan Henning Sommer, Wilhelm Barthlott, Mette Termansen, Gideon F. Smith, Simon Tokumine & James R. D. Taplin* 139

Jumping Genera: The Phylogenetic Positions of *Cassytha*, *Hypodaphnis*, and *Neocinnamomum* (Lauraceae) Based on Different Analyses of *trn*K Intron Sequences — *Jens G. Rohwer & Barbara Rudolph* 153

A Phylogenetic Study of the New World *Cleome* (Brassicaceae, Cleomoideae) — *Lupita Sánchez-Acebo* 179

Phylogeny and Geography of *Schefflera*: Pervasive Polyphyly in the Largest Genus of Araliaceae — *Gregory M. Plunkett, Porter P. Lowry II, David G. Frodin & Jun Wen* 202

A Revision of *Didymodon* Section *Fallaces* (Musci, Pottiaceae) in Europe, North Africa, Macaronesia, and Southwest and Central Asia — *Juan A. Jiménez, Rosa M. Ros, María J. Cano & Juan Guerra* 225

Taxonomic Additions for *Solanum* Section *Geminata* (Solanaceae) in Peru — *Sandra Knapp* 248

The *Stenobasipteron wiedemanni* (Diptera, Nemestrinidae) Pollination Guild in Eastern Southern Africa — *C. J. Potgieter & T. J. Edwards* 254

The Floral Biology of *Melasphaerula* (Iridaceae: Crocoideae): Is This Monotypic Genus Pollinated by March Flies (Diptera: Bibionidae)? — *Peter Goldblatt, John C. Manning & Peter Bernhardt* 268

Polyploidy in the Flora of the Hengduan Mountains Hotspot, Southwestern China — *Ze-Long Nie, Jun Wen, Zhi-Jian Gu, David E. Boufford & Hang Sun* 275

Cover illustration. *Megacorax gracielanus* S. González & W. L. Wagner, first described as a new genus and species of the family Onagraceae from Mexico in *Novon* 12: 362. 2002. The generic name is based on the combination of the Greek words *mega*, large or great, and *korax*, raven, to honor Missouri Botanical Garden Director Peter H. Raven, author of numerous papers and monographs on many aspects of the family and one of our foremost advocates for conservation and sustainable use of the environment. The specific epithet honors Graciela Calderón Díaz-Barriga, major contributor to *Flora del Valle de México* and *Flora del Bajío* and mentor of several generations of students. The illustration is by Alice R. Tangerini (U.S.).

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SYSTEMATICS AND EVOLUTION OF *LUDWIGIA* SECTION *DANTIA* (ONAGRACEAE)[1]

Ching-I Peng,[2] Clifford L. Schmidt,[3] Peter C. Hoch,[4] and Peter H. Raven[4]*

ABSTRACT

Ludwigia sect. *Dantia* is a polyploid complex ($x = 8$) of five species that are distributed mainly in the Coastal Plain of the southeastern United States, although two species, *L. palustris* and *L. repens*, have much broader ranges in North America and have become naturalized in Eurasia and elsewhere. All five species occur in wet habitats and often intermix; because the species generally lack well-developed pre- or post-zygotic barriers to hybridization, several of them commonly form natural hybrid populations. One particularly widespread hybrid involves *L. palustris* × *L. brevipes*, known in the literature as *L.* ×*lacustris*. Hybrids of *L. arcuata* × *L. repens* are common in Florida and, because they superficially resemble *L. brevipes*, have led to considerable confusion about the presence there of *L. brevipes*. *Ludwigia* sect. *Dantia* comprises one diploid, two tetraploid, and two hexaploid species. The genomic formula of the diploid *L. palustris* was designated as AA, and by means of a crossing program the genomes of other species were determined based on ability to form bivalents at meiosis in the hybrids. Of the two tetraploid species, only *L. spathulata* (AADD) has a genome of the extant diploid; *L. arcuata* (BBCC) is sharply distinct from *L. spathulata* in both morphology and genomic complements. The two hexaploid species, *L. brevipes* and *L. repens*, share the genomic formula AABBCC and appear to have been derived independently through hybridization between the diploid *L. palustris* (AA) and the tetraploid *L. arcuata* (BBCC). The substantial morphological differences between the two hexaploids may be related to the direction of the original crosses, since maternal influences are important in the group, as well as to the exact parental populations involved, subsequent selection history, and possibly backcrossing. Alternative evolutionary schemes are also discussed.

Key words: cytogenetics, hybridization, *Ludwigia* sect. *Dantia*, Onagraceae, systematics.

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[2] Herbarium, Research Center for Biodiversity, Academia Sinica, Nangang, Taipei 115, Taiwan.

[3] Department of Biological Sciences, San Jose State University, San Jose, California 95192, U.S.A.

[4] Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A.

* Author for correspondence: peter.hoch@mobot.org.

Ludwigia L. is the only genus of Onagraceae, tribe Jussiaeeae DC. (as "Jussieae"), a group that appears to be at least 50 million years old, based on the fossil record of its distinctive pollen (summarized in Raven, 1988) and perhaps as much as 80 Ma (Sytsma et al., 2004), and now determined by numerous independent analyses to be the sister group to the rest of Onagraceae (Eyde, 1977, 1981, 1982; Sytsma et al., 1991; Conti et al., 1993; Hoch et al., 1993; Lævin et al., 2003, 2004). *Ludwigia* consists of 81 species in 23 diverse sections (Raven, 1963a; Ramamoorthy & Zardini, 1987; Zardini & Raven, 1992), marked as monophyletic by at least two synapomorphies: absence of a floral tube that extends beyond the summit of the ovary (secondarily lost in *Chamerion* (Raf.) Raf. (Raven, 1976a; Baum et al., 1994)), and sepals persistent after abscission of petals and androecium (Raven, 1963a). Three other apomorphic character states occur in at least some species of *Ludwigia*, but their exact ontogeny remains uncertain: pollen in tetrads (some species and sections of *Ludwigia* have monads or polyads (Raven, 1963a); tetrads also occur in *Epilobium* L. and two species of *Camissonia* Link sect. *Lignothera* (P. H. Raven) P. H. Raven) (Raven, 1979), ovule archesporium single-celled, and outer integument dermal (both states also found in some genera of tribes Onagreae, Epilobieae, and Gongylocarpeae; Tobe & Raven, 1985, 1986b). The base chromosome number of *Ludwigia* ($x = 8$), unique in Onagraceae and formerly considered autapomorphic, may in fact be plesiomorphic (Levin et al., 2003), since it appears to be the base number in Lythraceae (Graham & Cavalcanti, 2001), which is sister to Onagraceae (Conti et al., 1997; Sytsma et al., 2004).

The fourth largest genus in Onagraceae (after *Epilobium*, *Oenothera* L., and *Fuchsia* L.), *Ludwigia* is unusual in having broad distributions in both subtropical and temperate wet habitats worldwide. South America, possibly the area of origin for the genus and family (Raven, 1963a, 1988), has ten endemic sections, North America has three, Africa five, and Asia three; two sections (sects. *Fissendocarpa* (Haines) Raven and *Oligospermum* (Micheli) Hara) are cosmopolitan (Raven, 1963a). Zardini and Raven (1992) provided a key to the sections of *Ludwigia*.

The three North American sections, section *Microcarpium* Munz (14 species), section *Dantia* (DC.) Munz (5 species), and section *Ludwigia* (4 species), are distributed mainly on the Coastal Plain of southeastern North America (Peng, 1989). These three sections differ from one another primarily in capsule morphology, habit, and phyllotaxy (Munz, 1944, 1965; Raven, 1963a; Peng, 1989), as well as in the presence and extent of polyploidy (Raven & Tai, 1979; Peng, 1988; Zardini et al., 1991). Section *Ludwigia* consists of four closely related and more or less interfertile diploid species (Raven & Tai, 1979), whereas sections *Microcarpium* and *Dantia* comprise diverse but morphologically distinct polyploid complexes (Raven & Tai, 1979; Peng, 1988, 1989). Biosystematic and taxonomic studies of section *Microcarpium* (Peng, 1988, 1989) addressed the evolutionary relationships among its 14 species, and new molecular analyses are in progress to further clarify the relationships of these three North American sections (C. Peng, in prep.).

This paper deals with the systematic and evolutionary relationships of *Ludwigia* sect. *Dantia*. It is intended as a companion paper to those on section *Microcarpium* (Peng, 1988, 1989) and section *Ludwigia* (Lutz, 1986, in prep.), and to the new molecular analyses, which together will summarize the systematics and relationships of the native North American sections of *Ludwigia*. We here combine results from earlier biosystematic studies within section *Dantia* (Schmidt, 1967) with additional crossing and cytogenetic analysis among the species, new fieldwork, and morphological study of extensive herbarium material.

Taxonomic History of Section *Dantia*

Table 1 summarizes the nomenclatural history of the species in section *Dantia* among major treatments of *Ludwigia*. The first species described in the modern section *Dantia* was the widespread *Ludwigia palustris* (L.) Elliott, originally named *Isnardia palustris* by Linnaeus (1753), based mainly on material from Europe. Elliott (1817) later transferred the species (and the genus *Isnardia*) to *Ludwigia*. The other widely distributed species in this group, *L. repens* J. R. Forst., was described next, in Forster's (1771) *Flora Americae Septentrionalis*, a work generally overlooked soon after its appearance. For example, apparently without seeing Forster's book, Swartz (1788) proposed the same binomial for this species, based on material from Jamaica. In addition, Elliott (1821) proposed the name *L. natans* for a collection of the same entity from South Carolina, and this latter name came into wide use (Torrey & Gray, 1840; Kuntze, 1891, as *Isnardia natans* (Elliott) Kuntze; Fernald & Griscom, 1935; Munz, 1944; Raven, 1963a), until Raven (1965) restored Forster's earlier name. However, Reveal et al. (2003) noted that the type specimen designated by Forster (*Clayton 775*) does not conform to Forster's description, and is in fact

Table 1. Comparison of historical treatments of species that have been included in *Ludwigia* sect. *Dantia*. As noted, *L.* ×*lacustris* is a natural hybrid (Raven & Tai, 1979); *L. verticillata* is a synonym for *L. inclinata* (L. f.) M. Gómez, now considered to be the monotypic section *Heterophylla* (Ramamoorthy, 1979; Praglowski et al., 1983).

	This paper	Raven (1963a) Munz (1965)	Munz (1944)	Small (1897)	Torrey & Gray (1840)	Candolle (1828)	Linnaeus (1753)
	Ludwigia Section	*Ludwigia* Section	*Ludwigia* Section		*Ludwigia* Section	*Isnardia* Section	
L. arcuata	*Dantia*	*Dantia*	*Ludwigiantha*	*Ludwigiantha*	*Ludwigiantha*	*Ludwigiaria*	—
L. brevipes	*Dantia*	*Dantia*	*Ludwigiantha*	—	—	—	—
L. ×*lacustris*	*Dantia*	*Dantia*	*Ludwigiantha*	—	—	—	—
L. repens	*Dantia*	*Dantia*	*Dantia*	*Isnardia*	*Isnardia*	*Ludwigiaria*	—
L. spathulata	*Dantia*	*Dantia*	*Dantia*	*Isnardia*	*Isnardia*	—	—
L. palustris	*Dantia*	*Dantia*	*Dantia*	*Isnardia*	*Isnardia*	*Dantia*	*Isnardia*
L. verticillata	*Heterophylla*	*Dantia*	*Ludwigiantha*	—	—	—	—

a specimen of *L. palustris* (L.) Elliott. In order to avoid disadvantageous nomenclatural change back to *L. natans*, Reveal et al. (2003) proposed conservation of *L. repens* with a conserved type; this proposal was approved (Brummitt, 2005).

In his *Flora Caroliniana*, Walter (1788) described two new species now in section *Dantia*, *Ludwigia arcuata* and *L. apetala*; Elliott (1817) submerged the latter into *L. palustris*. Michaux (1803) published *L. nitida* and *L. pedunculosa* from the Carolinas in his *Flora Boreali–Americana*, but Elliott (1817) synonymized the former with *L. palustris*, and questioned whether the latter might not be synonymous with *L. arcuata*, a view formally adopted by Torrey and Gray (1840).

Candolle (1828) reinstated an expanded genus *Isnardia*, and delimited two sections based on presence (sect. *Ludwigiaria* DC.) or absence (sect. *Dantia* DC.) of petals, including in it most of the taxa now included in *Ludwigia* sects. *Dantia*, *Ludwigia*, and *Microcarpium*. Candolle's classification led to an unnatural grouping of taxa from the three modern sections without regard for several critical differences in phyllotaxy, capsule morphology, and other characters. For example, the petaliferous, opposite-leaved *L. arcuata* and *L. repens* were classified with alternate-leaved members of modern sections *Ludwigia* and *Microcarpium* (some of which are not petaliferous as Candolle described) in his section *Ludwigiaria*. His section *Dantia* likewise combined a divergent group of *Ludwigia* species from modern sections *Dantia* and *Microcarpium*.

Torrey and Gray (1840) re-merged *Isnardia* with *Ludwigia*, and divided the native North American *Ludwigia* species into three sections. Their section *Euludwigia* comprised all species then known of what we now recognize as sections *Ludwigia* and *Microcarpium*. They split the modern section *Dantia* into section *Isnardia* (with *L. palustris*, *L. repens* [as *L. natans*], and a new species, *L. spathulata*) and section *Ludwigiantha* (with only *L. arcuata*), based on petal presence/absence, peduncle length, capsule shape, and prominence of nectary disc (their "stylopodium"). Small (1897) emphasized these characters even more in elevating *Ludwigiantha* to generic status, to which Long (in Britton & Brown, 1913) added a new species, *Ludwigiantha brevipes*. Eames (1933) combined *Ludwigiantha* with *Ludwigia*, and proposed another new species, *L. lacustris*, with flowers smaller than those of *L. brevipes* and ovaries "fertilized . . . rarely, or late" (Eames, 1933: 229).

In a comprehensive study of native North American *Ludwigia*, Munz (1944) recognized Candolle's (1828) section *Dantia*, with modifications. For apetalous taxa, he removed the erect, spiral-leaved plants to his new section *Microcarpium*, retaining in section *Dantia* only the prostrate, opposite-leaved plants. Munz also recognized Torrey and Gray's (1840) section *Ludwigiantha* to include the prostrate, opposite-leaved, conspicuously petaliferous *L. arcuata*, *L. brevipes*, *L. lacustris*, and a new species, *L. verticillata* Munz.

In his synopsis of *Ludwigia*, Raven (1963a) combined Munz's sections *Ludwigiantha* and *Dantia*, a treatment later adopted by Munz (1965), and argued against recognition of infraspecific taxa in *L. palustris*. Schmidt (1967) and later Raven and Tai (1979) showed that, of the seven species listed by Raven (1963a) and Munz (1965) in section *Dantia*, *L. lacustris* was a sterile natural hybrid between the hexaploid *L. brevipes* and the diploid *L. palustris* (hereafter referred to using the convention "*L.* ×*la-*

custris"), and *L. verticillata* was synonymous with *L. inclinata* (L.f.) M. Gómez, now placed in the monotypic section *Heterophylla* Ramamoorthy, in which leaves on the lower, prostrate branches are verticillate, whereas those on the upper flowering branches are spirally arranged (Ramamoorthy & Zardini, 1987). Kasselmann (2003) chose to emphasize the verticillate nature of some populations as *L. inclinata* var. *verticillata* (Munz) Kasselmann. Therefore, in this paper we recognize a total of five species in section *Dantia* (*L. arcuata, L. brevipes, L. palustris, L. repens,* and *L. spathulata*), one named hybrid (*L.* ×*lacustris*), and several other persistent natural hybrids.

In the widespread species *Ludwigia palustris* and *L. repens*, several infraspecific taxa have been proposed previously (Candolle, 1828; Grisebach, 1866; Fernald & Griscom, 1935) owing to the great variation in these species in such characters as leaf and sepal shape, capsule size, and bracteole and pedicel length. As Duke (1955) and Raven (1963a) suggested, the variations are indistinct and/or continuous, and appear to be primarily ecological or ecotypic in nature, without any clear geographical component. Crosses between morphologically divergent populations in both species failed to reveal any significant genomic differentiation; all crosses showed normal chromosome pairings in both species. In view of these relationships, we choose not to recognize any infraspecific taxa in these species.

Morphological Characters

Peng (1989: table 1) summarized some diagnostic morphological characteristics of the three North American sections *Dantia, Ludwigia,* and *Microcarpium*. Raven (1963a) and Munz (1965) suggested that section *Dantia* shares with the other native North American sections the apomorphic character state of haplostemony (stamens as many as sepals) versus diplostemony (stamens twice as many as sepals), the condition found throughout most of the rest of Onagraceae. This condition of haplostemony is also found in several African and Asian sections, but it is not known if they derived this condition independently of the North American sections. Among the sections of *Ludwigia* with haplostemony, the three North American sections (sects. *Dantia, Ludwigia,* and *Microcarpium*) share two other possibly apomorphic character states: (1) seeds pluriseriate and free, and (2) nectaries glabrous and convex (Eyde, 1981); this combination of states is otherwise found only in *L. ovalis* Miq., comprising the monotypic section *Miquelia* Raven of East Asia and considered to be closely related to the North American sections (Raven, 1963a). The species of section *Dantia* also share with section *Miquelia* and 8 of the 14 species of section *Microcarpium* the character state of thick seed endotesta (Tobe et al., 1988), but more information about the homology and distribution of this character is needed (Hoch et al., 1993). The synapomorphy that delimits section *Dantia* from the rest of this north temperate haplostemonous group is the presence of opposite to whorled, rather than alternate, leaves (Munz, 1965; Zardini & Raven, 1992), and indeed this character is virtually unique in the genus, supporting the monophyly of the five species of section *Dantia*. Table 2 provides a brief comparison of diagnostic features among species of *Ludwigia* sect. *Dantia*; detailed discussions of these characters are given below.

Habit and stem. All species of *Ludwigia* sect. *Dantia* are herbaceous perennials with slender repent stems more or less ascending at the tips (Fig. 1). They are usually well-branched, forming small to large colonies on moist ground. Plants are sometimes submerged, but flowering always takes place on emergent stems. The submerged stems of section *Dantia* are never swollen and spongy like those of sections *Ludwigia* and *Microcarpium* (Peng, 1989), nor do they ever have spongy white pneumatophores like some members of section *Oligospermum* (Raven, 1963a). When the plants occur around swamps and lakes or along ditches, they tend to creep up the muddy banks instead of floating on the water.

Pubescence. Of the five main types of vestiture found in species of *Ludwigia* sect. *Microcarpium* (Peng, 1989), species of section *Dantia* have three: strigillose, minutely strigillose, and minutely papillose. Perhaps the most distinctive species is *L. spathulata*, which is densely strigillose throughout the stem, leaves, and inflorescence, with appressed hairs 0.25–0.7 mm long. *Ludwigia palustris, L. brevipes,* and *L. repens* are generally glabrous except for the leaf margins, sepals, bracteoles, and fruit surfaces, which are minutely strigillose, with appressed hairs 0.02–0.1 mm long. Plants of *L. arcuata* are similar, but slightly more densely pubescent. *Ludwigia arcuata* also uniquely has very short appressed hairs (minutely strigillose) between or on the disc lobes. The capsule walls of *L. brevipes* are sometimes covered with minute, erect protuberances slightly longer than the "minutely papillose" vestiture found, for example, in *L. glandulosa* Walter and *L. lanceolata* Elliott of section *Microcarpium* (Peng, 1989).

Leaves. The opposite leaves of section *Dantia* (Fig. 1) are a main diagnostic feature and apparent

Table 2. Morphological comparison and diagnostic features of species in *Ludwigia* sect. *Dantia*.

	L. palustris	*L. spathulata*	*L. arcuata*	*L. brevipes*	*L. repens*
Overall pubescence	Glabrous; minutely strigillose on margins of leaves, sepals, and on capsule surface	Densely strigillose throughout	Subglabrous to sparingly strigillose	Glabrous; minutely papillose-strigillose on margins of leaves, sepals, bracteoles, and on capsule wall	Glabrous; minutely papillose-strigillose on margins of leaves, sepals, bracteoles, and on capsule wall
Leaf shape (emergent)	Narrowly to broadly elliptic or ovate-elliptic	(Narrowly) elliptic spatulate	Narrowly elliptic or oblanceolate-elliptic to sublinear	Oblanceolate-elliptic to narrowly oblanceolate	Narrowly elliptic to broadly lanceolate-elliptic to suborbiculate
length × width (mm)	5.5–45 × 2.5–23	9–17 × 3.3–9	6–18 × 1.2–5	(7–)10–17(–20) × 2–7(–10.5)	8–45 × 4–27
Sepal shape	Ovate-deltate	Broadly ovate to deltate	Narrowly triangular	Triangular (narrowly)	Ovate-deltate (narrowly)
length (mm)	1.1–2	1–1.7	5.2–10	(3.5–)4–5(–5.8)	1.8–5
width (mm)	1–2.1	1.1–1.7	1.5–2.7	1.7–2.8	1.5–3.5
length : width	1	1	3–4	2	1
Petals +/−	−	-	+	+	+
Petal length (mm)	—	—	7–11	4.5–5.2	1.1–3
Anther length (mm)	0.2–0.4	0.2–0.35	1.3–2	0.75–1	0.4–0.9
Filament length (mm)	0.4–0.6	0.5–0.8	2.5–4.5	1.8–2.5	0.5–1.5
Pollen (S)ingle/(T)etrads	S	S	T (tight)	T (loose)	T or S
Style length (mm)	0.35–0.7	0.25–0.5	2.3–4(–4.8)	1.1–1.7	0.6–0.9
Nectary disc height	0.15–0.3	0.1–0.15	0.6–1	0.55–0.7	0.3–0.8
Capsule shape	Oblong-obovoid or oblong with abruptly constricted base	Oblong-obovoid	Clavate, sometimes curved	Clavate, sometimes curved	Elongate-obpyramidal or oblong with attenuated base
surface with (+) or without (−) green bands	+	+	−	−	−
length (mm)	(1.6–)2–5	2.5–4(–4.5)	5.5–10	6–10.5	4–10
thickness (mm)	1.5–3(–3.5)	1.5–2.5	2.3–4	(2–)2.5–4	2.5–3.7
Pedicel length (mm)	0–0.5	0–0.5	(12–)17–45	(4.5–)6–15(–20)	0–3
Bracteole length (mm)	0.25–1(–1.8)	0.2–0.8	1.4–5	1–3(–4.5)	1–5(–8)
Seed color	Yellowish	Dark reddish brown	Light to dark brown	Light to dark brown	Yellowish
Seeds/capsule (N = 10)					
Range (mean)	80–149 (114)	29–59 (45)	202–321 (253)	82–217 (146)	54–92 (71)

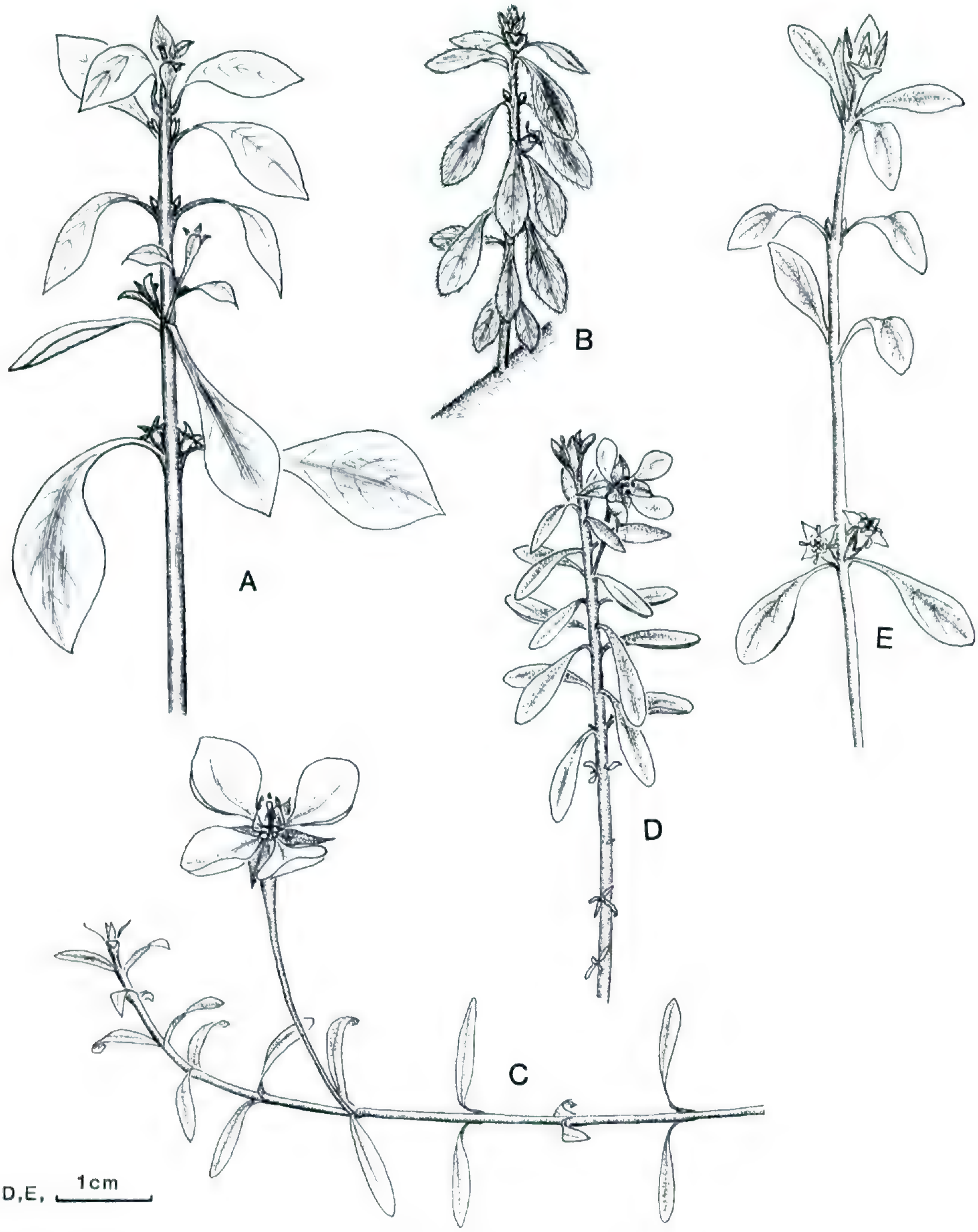

Figure 1. Habit of species in *Ludwigia* sect. *Dantia*. —A. *L. palustris*. —B. *L. spathulata*. —C. *L. arcuata*. —D. *L. brevipes*. —E. *L. repens*.

synapomorphy of the group. The only exceptions occur in some populations of *Ludwigia palustris* in the Hawaiian Islands, Haiti, Namibia, and New Zealand, in which the leaves may be both alternate and opposite. In other respects, however, these plants cannot be distinguished from typical *L. palustris*.

Leaf shape in section *Dantia* ranges from very narrowly to broadly elliptic, ovate- or obovate-elliptic to narrowly spatulate. In *Ludwigia palustris* (Fig. 1A) and *L. repens* (Fig. 1E), leaf shape is extremely variable, encompassing much of the total variation among all species. By contrast, leaf shape in *L. spathulata* (Fig. 1B) is uniformly elliptic-spatulate to narrowly so, with an attenuate base; this shape, and its dense pubescence, is diagnostic for this species. Leaves of *L. brevipes* (Fig. 1D) are somewhat similar in shape to those of *L. spathulata*, but are usually narrower, with a narrowly cuneate base, and also are glabrous to sparsely strigillose. Plants of *L. arcuata* characteristically have very narrowly elliptic to sublinear leaves (Fig. 1C).

When growing in submerged conditions, plants of *Ludwigia palustris* and *L. repens* tend to form elliptic to subrotund leaves that are larger and broader than the aerial leaves. Submerged leaves of *L. arcuata* and *L. brevipes*, on the other hand, tend to be nearly linear. The fifth species, *L. spathulata*, is rarely submerged, or at least has no attendant morphological specializations.

Species of section *Dantia*, like most *Ludwigia*, have subentire leaf margins, with a few glandular reddish teeth of hydathodal structure (Castells et al., 1979; Keating, 1982). Leaf anatomy of section *Dantia* is moderately specialized within the family (Keating, 1982), with little or no adaxial ridge, less prominent rounding abaxially, a midvein consisting of a more or less broad arc, absence of adaxial phloem, and in smaller leaves a continuous palisade layer across the adaxial side of the midrib. Several other sections in *Ludwigia* share one or more of these specializations. Keating (1982) reported styloids or coarse raphides oriented vertically in the mesophyll of *L. palustris*, whereas they are usually horizontal in mid-mesophyll of other species of *Ludwigia*.

Pedicels. Flowers and fruits are subsessile in *Ludwigia palustris* (Figs. 1A, 2A), *L. spathulata* (Figs. 1B, 2B), and most collections of *L. repens* (Figs. 1E, 2E), whereas they are distinctly pedicellate in *L. arcuata* (Figs. 1C, 2C), *L. brevipes* (Figs. 1D, 2D), and some populations of *L. repens* (Table 2). Pedicels of *L. arcuata* (12–45 mm long) are the longest in section *Dantia*. Pedicels are ascending to suberect, never as elsewhere in the genus recurved in bud (*L. brachyphylla* (Micheli) Hara, sect. *Myrtocarpus* (Munz) Hara) or in fruit (*L. decurrens* Walter, sect. *Pterocaulon* Ramamoorthy) (Ramamoorthy & Zardini, 1987).

Bracteoles. Subopposite bracteoles are present in all species of *Ludwigia* sect. *Dantia* (Fig. 2), flanked at the base by a pair of minute, reddish or dark purplish, gland-like trichomes. The shape of the bracteoles varies from narrowly lanceolate, elliptic, or oblanceolate to linear. In the apetalous, small-flowered *Ludwigia palustris* and *L. spathulata*, the bracteoles are 0.2–1(–1.8) mm long, whereas in the petaliferous, larger-flowered *L. arcuata*, *L. brevipes*, and *L. repens*, they are 1–5(–8) mm long. Bracteoles occur variously from the upper part of the pedicel to nearly halfway up the ovary/capsule.

Flowers. As in most species of *Ludwigia*, the flowers are borne in leaf axils of the stems (Figs. 1, 2). All species of section *Dantia* are 4-merous, and three of the five species are petalous. The apetalous *L. palustris* and *L. spathulata* tend to produce more flowers per individual than the petalous species, but precise comparisons have not been made.

Sepals. Sepals are entire, ovate-deltate or deltate to narrowly triangular. As is characteristic of the entire genus (Raven, 1963a; Munz, 1965), the sepals persist even after the capsules mature and dehisce. Sepal size can be diagnostic; for example, sepal length is 1–2 mm in the apetalous species *Ludwigia palustris* and *L. spathulata*, 1.8–5 mm in *L. repens*, (3.5–)4–5(–5.8) mm in *L. brevipes*, and 5.2–10 mm in *L. arcuata*. The sepal length/width ratio is about 1:1 in *L. palustris*, *L. spathulata*, and *L. repens*, 2:1 in *L. brevipes*, and 3–4:1 in *L. arcuata* (Table 2).

Petals. Four yellow petals are present in the flowers of *Ludwigia arcuata* (Fig. 2C), *L. brevipes* (Fig. 2D), and *L. repens* (Fig. 2E). They are usually elliptic to spatulate, obovate, or oblanceolate. The petals are largest in *L. arcuata* (7–11 mm long), smaller in *L. brevipes* (4.5–5.2 mm long) and *L. repens* (1.1–3 mm long). In *L. repens*, the petals are often variable in shape and size even in the same flower; although they sometimes are vestigial, they are never completely lacking, as reported by Gleason (1952). As is the case in section *Microcarpium*, the petals fall off a few hours after anthesis, which commences early in the morning, and are usually gone by noon. For this reason, even herbarium specimens of petaliferous species of section *Dantia* frequently lack petals on open flowers.

The absence of petals appears to be an advanced condition in *Ludwigia* sect. *Dantia*, but one whose expression is not always complete. Extra stamens and rudimentary petals occasionally appear in the apetalous *L. palustris*; a specimen from Costa Rica (Tres Ríos, Cartago, *Raven 20419*, DS), grown in the greenhouse, produced a flower with two extra appendages in the normal position of petals, one stamen-like and the other petal-like. Similarly, flowers on a plant of the normally apetalous *L. spathulata* in cultivation also produced a single petal.

Stamens. Flowers of *Ludwigia* sect. *Dantia* are consistently haplostemonous, bearing four stamens in one whorl (Fig. 2), like those of several other groups of *Ludwigia* including section *Microcarpium*; the rest of the genus is diplostemonous with two distinct whorls (Raven, 1963a), like a majority of the family. The stamens are antesepalous, situated between the sepal base and the nectary disc. Although species of section *Dantia* have only one whorl of four stamens, some hybrids between petalous and apetalous plants have a second whorl of stamens or an intermediate number of stamens. The extra stamens were either petaloid with dilated fil-

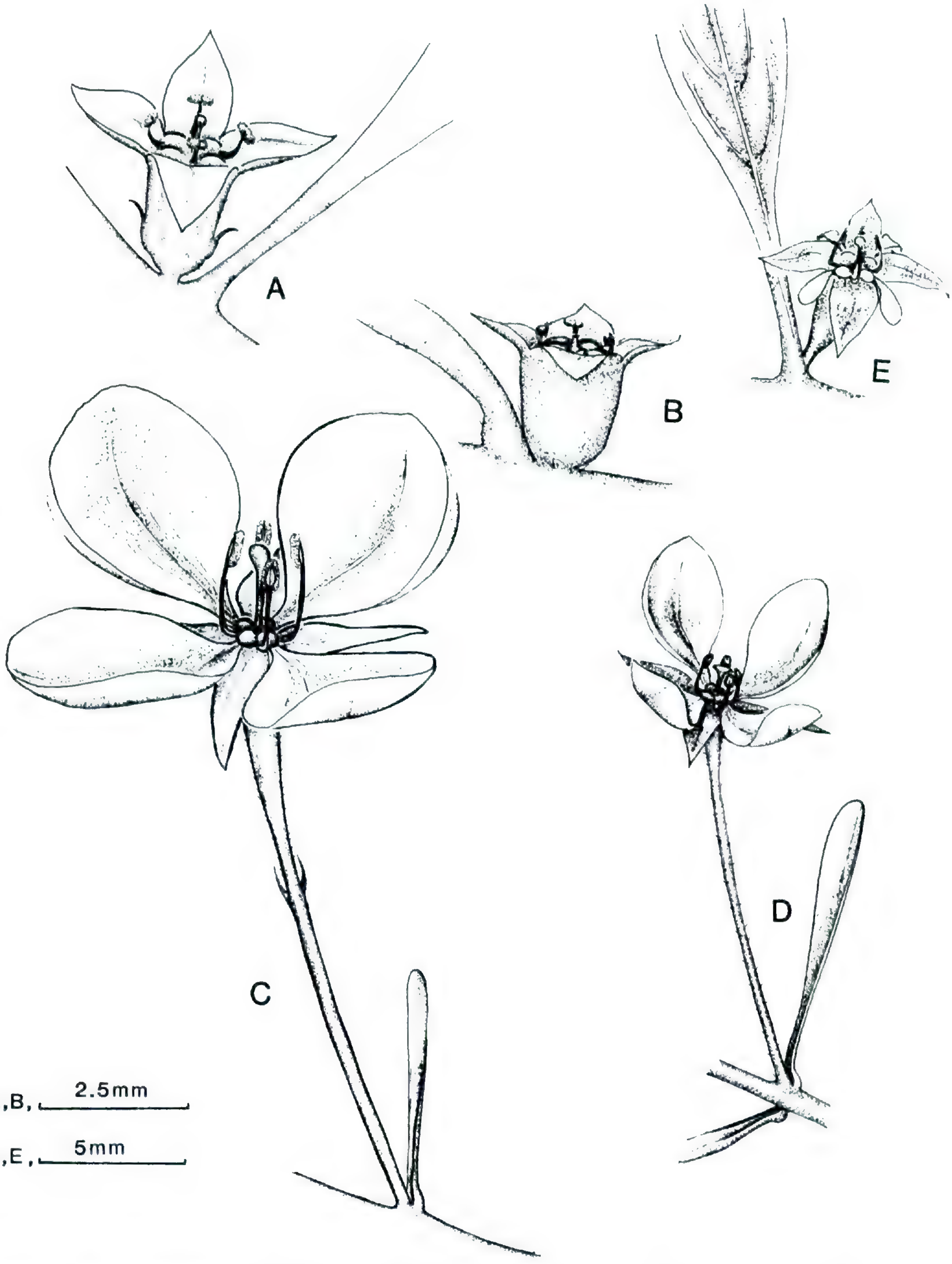

Figure 2. Floral morphology of species in *Ludwigia* sect. *Dantia*. —A. *L. palustris*. —B. *L. spathulata*. —C. *L. arcuata*. —D. *L. brevipes*. —E. *L. repens*.

aments or more normal, except that the filaments were longer and the anthers smaller. These additional stamens occurred in the normal position of the petals. These observations may support the hypothesis that in many families, including Onagraceae, petals represent sterilized stamens, specialized for the attraction of insects.

Anther length varies from 0.2–0.35 mm long in *L. spathulata* to 1.3–2 mm long in *L. arcuata*. In their study of polysporangiate anthers, Tobe and Raven (1986a) reported that anthers of *L. repens*, the only species examined from section *Dantia*, did not have transverse septa in their sporogenous tissue, a feature found in at least some taxa of every

genus of Onagraceae examined. Several other species of *Ludwigia* also lacked septa, although Tobe and Raven (1986a: 477) suggested that septa "may actually be present, but in very low frequency."

Pollen. The specialized structure of the pollen wall (Skvarla et al., 1976) and the presence of viscin threads (Skvarla et al., 1978) in Onagraceae are two strong synapomorphies for the family (Raven, 1979, 1988; Hoch et al., 1993), and pollen characters can be diagnostic at the generic and/or infrageneric level. For example, all species of *Ludwigia* have smooth viscin threads (Praglowski et al., 1983), which distinguish the genus from most others, but this character is not diagnostic among sections or species. On the other hand, species of *Ludwigia* release their pollen either in monads, tetrads, or polyads (Skvarla et al., 1975; Praglowski et al., 1983), and most sections can be characterized by just one type of release. However, both sections *Dantia* and *Microcarpium* are mixed for this character, releasing pollen in either monads or tetrads. In section *Dantia*, the larger-flowered, petaliferous species shed their pollen in tetrads, whereas the apetalous species (*L. palustris* and *L. spathulata*) shed their pollen as monads. *Ludwigia arcuata*, with the largest flowers, consistently sheds pollen in tight tetrads. In *L. brevipes* and particularly in *L. repens*, the tetrads have a tendency to disassociate easily (Skvarla et al., 1975; Praglowski et al., 1983). In other pollen morphological features, section *Dantia* is quite similar to section *Microcarpium*: both have isopolar grains with frequently prominent colpal extensions and a psilate exine (Praglowski et al., 1983).

Disc. The nectary disc consists of four semicontiguous rounded lobes that are elevated at the summit of the ovary. According to Eyde (1981), these raised, hairless nectaries are apomorphic within *Ludwigia*. They are best developed in *Ludwigia arcuata* (Fig. 23h) and *L. brevipes* (Fig. 25i), in which the disc consists of four protuberant hemispheres around a sunken style base. An overemphasis on the degree of prominence of the disc and on other minor characters resulted in excessive splitting of these species of *Ludwigia* and in the recognition of *Ludwigiantha* as either a section of *Ludwigia* (Torrey & Gray, 1840) or a segregate genus (Small, 1897; Britton & Brown, 1913) to accommodate the species with very prominent nectary discs, especially *L. arcuata*. The nectary is glabrous except in some populations of *L. arcuata*, where it may be minutely strigillose between or on the disc lobes. Species with more prominent discs appear to secrete more nectar than those with smaller ones, but no actual measurements were made.

Capsules. Capsule morphology is diverse in *Ludwigia* (Fig. 3; Raven, 1963a; Eyde, 1978; Peng & Tobe, 1987; Peng, 1988, 1989) and often provides useful taxonomic characters. In section *Dantia*, *L. palustris* (Fig. 3A) and *L. spathulata* (Fig. 3B) have capsules that are small (1.6–5 mm long), oblong-ovoid to oblong-obovoid, thin-walled, and sessile or nearly so. Those of *L. arcuata* (Fig. 3C) and *L. brevipes* (Fig. 3D) are larger (5.5–10.5 mm long), clavate and sometimes curved, thick-walled, on pedicels (4.5–)6–45 mm long. Capsules in *L. repens* (Fig. 3E) are 4–10 mm long, elongate-obpyramidal or oblong with attenuate bases, thick-walled, sessile or on pedicels up to 3 mm long. Eyde (1978) reported that in *L. palustris*, the parenchyma opposite the locule is less than 10 cells thick, and these cells remain small during fruit development while the cells in the septal radii enlarge. At fruit maturity, the tissue of the placental radii is so thin in *L. palustris* and usually also in *L. spathulata* that outlines of the seeds are often visible through the capsule walls. The exocarp appears greenish in these thin areas in the placental radii against a tan background.

Salisbury (1972) noted that in England fruits of *Ludwigia palustris* become detached when ripe and fall to the ground or water surface. This also occurs in North American populations of *L. palustris* and other species in section *Dantia*. In all species, the detached capsules eventually decay or rupture. In *L. palustris* and *L. spathulata*, seeds may scatter from the capsule, or may germinate in situ through the fragile, paper-thin areas of the exocarp. In *L. arcuata*, *L. brevipes*, and *L. repens*, with thick-walled capsules, the exocarp forms irregular cracks and breaks apart, resembling the "peeled dehiscence" that characterizes species such as *L. glandulosa* of section *Microcarpium* (Peng & Tobe, 1987). At that stage, the capsules are readily crushed and the seeds easily released.

Seeds. In all species of *Ludwigia* sect. *Dantia*, seeds are free and pluriseriate in each locule of the capsule, with a narrow raphe. They are small (0.5–0.8 mm long, 0.3–0.45 mm thick) and generally ellipsoidal, mostly yellowish to brown or dark brown, or even dark reddish brown in *L. spathulata*. Because all of the species have seeds of similar size, differences in capsule size mainly depend on variation in the number of seeds per capsule (Table 2). So *L. arcuata*, with capsules 5.5–10 mm long, has on average 253 seeds per capsule; by contrast, *L. spathulata*, with capsules 2.5–4(–4.5) mm long, has only 45 seeds per capsule. The other taxa are intermediate in capsule size and seed number;

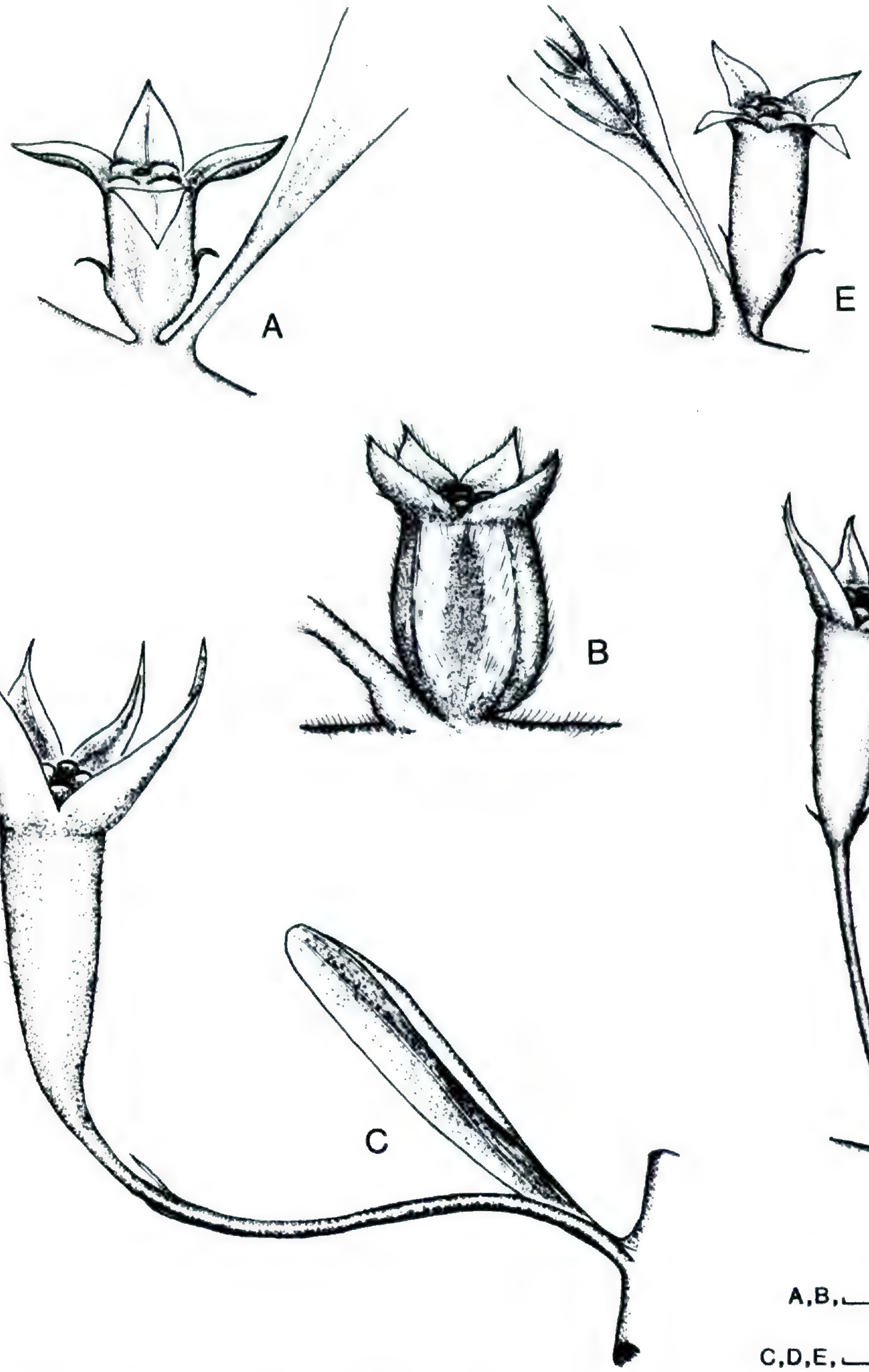

Figure 3. Capsule morphology of species in *Ludwigia* sect. *Dantia*. —A. *L. palustris*. —B. *L. spathulata*. —C. *L. arcuata*. —D. *L. brevipes*. —E. *L. repens*.

these numbers are based on one capsule counted on each of ten plants per species (Schmidt, 1967).

Tobe et al. (1988) examined seed coat anatomy in *Ludwigia* sects. *Microcarpium*, *Dantia*, and *Miquelia* (and two fossil seeds from Europe), and found that all species of section *Dantia* have conspicuously thickened endotesta, an apomorphic character state also found in section *Miquelia* and some species of section *Microcarpium*. Based on this feature, Tobe et al. (1988) suggested that taxa of section *Dantia* were derived from an ancestral stock within section *Microcarpium*, although Peng (1989) later questioned that hypothesis. Seeds of species of section *Dantia* resemble those of section

Table 3. Voucher information for populations of species of *Ludwigia* sect. *Dantia* used in experimental hybridizations. Due to the morphological variability and wide geographical ranges of *L. palustris* and *L. repens*, three strains each of those taxa (designated a–c) were employed in the crossing program. Except as noted, we used strain "a" of each species in interspecific crosses.

Ludwigia arcuata Walter (n = 16)	U.S.A. Florida: Leon Co., near Tallahassee, *Godfrey 62861* (DS).
Ludwigia brevipes (Long) Eames (n = 24)	U.S.A. North Carolina: Robeson Co., 3.2 mi. W of Lumberton, *Lloyd 1030* (DS).
Ludwigia palustris (L.) Elliott (n = 8)	(a) U.S.A. Arkansas: Clark Co., Terre Noir Creek bottoms, *Demaree 48955* (DS). (b) U.S.A. North Carolina: Cumberland Co., 8 mi. N of Fayetteville, *Lloyd 1025* (DS). (c) U.S.A. California: Sonoma Co., Laguna de Santa Rosa, *Rubtzoff s.n.* (*Raven 18068*, DS).
Ludwigia repens J. R. Forst. (n = 24)	(a) U.S.A. Florida: Orange Co., near Lake Tsala Apopka, *Raven 17932* (DS). (b) U.S.A. California: San Bernardino Co., Lost Lake, Lone Pine Canyon, *Raven 16681* (DS). (c) MEXICO. Nuevo León: Reó Ramas, between Monterrey and Linares, *Hitchkiss & Tindale s.n.* (*Raven 19634*, DS).
Ludwigia spathulata Torr. & A. Gray (n = 16)	U.S.A. Florida: Leon Co., ca. 2 mi. N of Woodville, *Godfrey 62880* (DS).

Microcarpium in shape, size, and coloration, but lack the great diversity in surface cell orientation found in section *Microcarpium* (Peng, 1989). The seed surface cells in all species of section *Dantia* are consistently transversely elongate to the seed length (Eyde 1978: fig. 25), with minor variation on the two ends and around the raphe.

Cytology and Reproductive Biology

The basic chromosome number of *Ludwigia* is established as x = 8, with no aneuploidy but extensive polyploidy (Kurabayashi et al., 1962; Raven & Tai, 1979; Peng, 1988; Zardini et al., 1991). The first cytological study of section *Dantia* by Gregory and Klein (1960) reported gametic chromosome numbers in three of the five species and first documented polyploidy in section *Dantia*. Schotsman (1970) and Queirós (1976) subsequently confirmed n = 8 in *L. palustris*. Raven and Tai (1979) reported chromosome numbers for 27 populations of all five species of section *Dantia*, including all nine parental strains used in this biosystematic study (vouchers listed in Table 3). To summarize data from these studies, *L. palustris* is diploid (n = 8), *L. spathulata* and *L. arcuata* are tetraploid (n = 16), and *L. brevipes* and *L. repens* are hexaploid (n = 24).

Meiotic chromosome configurations and self-compatibility were determined on all populations sampled and brought into cultivation for this study, which includes all five species (Table 3) and several natural hybrids (Schmidt, 1967). We have observed natural populations of all species in the field to elucidate their reproductive biology.

All members of section *Dantia* are genetically self-compatible, although most strains outcross regularly in nature. Shortly after the flowers open in the morning, the subglobose stigma becomes sticky and receptive. The anthers usually dehisce at the same time or slightly later, but are initially held away from the stigma in both petalous and apetalous species by the ascending filaments. The filaments gradually arch over toward the center of the flower and the anthers become firmly attached to the sticky stigma, usually by midday, thus effecting self-pollination. Cross-pollination is possible if insects visit the flowers for nectar in the intervening period. In some populations of *Ludwigia arcuata*, however, the stigma is elevated above the anthers, which physically prevents self-pollination.

In section *Dantia*, the occurrence of certain characters in various combinations is associated with cross-pollination. These include showy flowers with large, yellow petals and long pedicels; large anthers with abundant pollen shed in tight tetrads; prominent nectary disc with copious nectar; anthers held away from the stigma for longer periods; and stigma exserted beyond the anthers. These features are most fully exhibited by the tetraploid *Ludwigia arcuata*, somewhat less by the hexaploid *L. brevipes*, and only occasionally or not at all by other species.

Conversely, certain characters associated with

self-pollination are found in the diploid *L. palustris* and the tetraploid *L. spathulata*: small, greenish, apetalous, and subsessile flowers; small anthers with pollen shed singly; inconspicuous nectary disc with low nectar production; and anthers held close or attached to the receptive stigma soon after anthesis. The hexaploid *Ludwigia repens* is intermediate between these two morphological extremes: the flowers have small petals, short but distinct pedicels, and pollen tetrads that easily disassociate in many strains.

Observations of plants in the field and in cultivation showed that flowers of *Ludwigia arcuata* and *L. brevipes* attracted abundant bees, wasps, and ants, although these have not been further identified or quantified. We have not observed any insects on flowers of the other three species in section *Dantia*. However, it does appear that the less conspicuous flowers of those species may be visited by insects at least occasionally, judging by the occurrence of confirmed natural intersectional and intrasectional hybrid populations involving the apetalous species as putative parents (see below).

Ecology and Geographical Distribution

As is true in general for *Ludwigia*, species of section *Dantia* grow in at least seasonally wet habitats. They most often are found creeping and forming mats along roadside ditches, margins of pools, ponds, or lakes, riverbanks or dried up river bottoms, edges of swamp forests, swampy prairies, or disturbed savannas.

Species of section *Dantia*, like those of sections *Ludwigia* and *Microcarpium* (Peng, 1988), occur primarily in the Coastal Plain of the United States, which is defined geologically as the flat, low-lying region between the Atlantic and Gulf coasts and the Piedmont and Central Highlands, and extending from southern New England south along the Atlantic Coast and west along the Gulf of Mexico to the Mexican border (Peattie, 1922). *Ludwigia brevipes* (Fig. 22), *L. arcuata* (Fig. 24), and *L. spathulata* (Fig. 22) are endemic to the southeastern United States. *Ludwigia repens* is common in that region and on into the savannas of central Texas, and is scattered into the southwestern states (Fig. 27) and the Caribbean Islands (Fig. 28); it also is sporadically naturalized in India (Khan, 1977) and Japan (Murata & Peng, 1988). *Ludwigia palustris*, one of the most widespread species in the genus, is distributed over much of the United States and southern Canada excluding the northern Great Plains and the western montane regions, extending southward through Mexico and Central America to Colombia and Venezuela in South America, common also in Europe and Africa, and introduced in the Hawaiian Islands and New Zealand.

Sympatric Occurrence and Natural Hybridization

Natural hybrids between members of *Ludwigia* sect. *Dantia*

Because of its wide range, *Ludwigia palustris* significantly overlaps in distribution with all four other species of section *Dantia*. The distribution of *L. repens* also overlaps the others, but less so in the case of *L. spathulata*, a rare species found primarily in the Coastal Plain of southern Alabama, the panhandle of Florida, and extreme southwestern Georgia. *Ludwigia spathulata* is well separated from *L. brevipes*, an uncommon species found mainly from South Carolina to southern Virginia, and scarcely overlaps the range of *L. arcuata*. At its northern limit in southern South Carolina, *L. arcuata* approaches the southern extent of *L. brevipes*. In part, it was the high level of sympatry among the species and the apparent frequency of natural hybridization that drove the initial decision to carry out biosystematic analyses in *Ludwigia* sect. *Dantia*.

In addition to having variously overlapping geographical ranges, all species of section *Dantia* grow in similar moist habitats, have substantially overlapping flowering seasons, are self-compatible yet capable of outcrossing, and appear to be visited by generalist bees, wasps, and ants. Since post-zygotic barriers to hybridization are poorly developed or absent (Schmidt, 1967; Peng, 1988), as discussed elsewhere, these factors facilitate the occurrence of natural hybridization.

A comparison of the morphological and cytological features of suspected natural hybrids with those of the experimental hybrids confirms that natural interspecific hybridization is apparently common in section *Dantia* (Schmidt, 1967). Natural hybrid populations occur in most instances where two species overlap in their distribution ranges (cf. Figs. 4, 5, 19, 20, 22, 24, 27, 28).

Putative natural hybrids are often identifiable due to their morphological intermediacy. Overall patterns of vestiture, leaf shape, presence or absence of petals, sepal shape and size, length of stamens and style, pollen viability and method of shedding (in monads or tetrads), condition of ovary (aborted or well-developed), capsule morphology, and pedicel length provide the best diagnostic features. Chromosome number and meiotic chromosome pairing behavior in most cases offer conclusive evidence of the hybridity of plants. Discussion

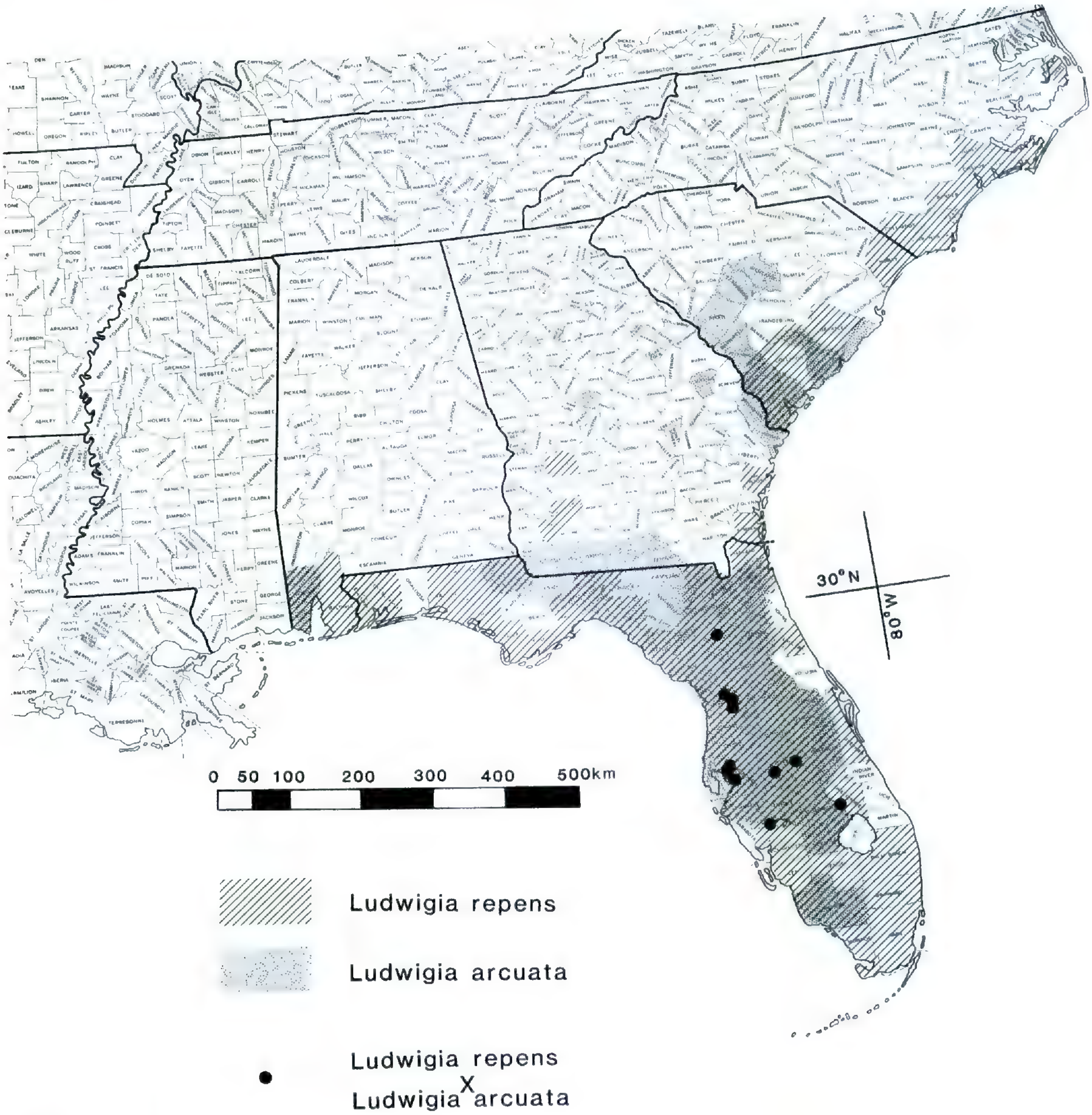

Figure 4. Distribution of the natural hybrids *Ludwigia arcuata* × *L. repens* relative to the ranges of the parental species (range of *L. repens* is shown in part).

of specific natural hybrid combinations, including voucher information, follows the systematic treatment of accepted taxa. The following alphabetical list enumerates verified natural hybrids among species of *Ludwigia* sect. *Dantia*.

Ludwigia arcuata ($n = 16$) × *L. repens* ($n = 24$)
Ludwigia brevipes ($n = 24$) × *L. palustris* ($n = 8$) [*Ludwigia* ×*lacustris*]
Ludwigia brevipes ($n = 24$) × *L. repens* ($n = 24$)
Ludwigia palustris ($n = 8$) × *L. repens* ($n = 24$)
Ludwigia palustris ($n = 8$) × *L. spathulata* ($n = 16$)

NATURAL HYBRIDS BETWEEN MEMBERS OF *LUDWIGIA* SECTS. *DANTIA* AND *MICROCARPIUM*

Three of the five species in *Ludwigia* sect. *Dantia* are known to form natural hybrids with at least 6 of the 14 species in section *Microcarpium* in areas where they co-occur (Peng, 1988). Certain features, such as high pollen and fruit sterility, suberect stems with some prostrate branches, and either subopposite leaves or mixed opposite and alternate leaves on the stems, are usually diagnostic of such intersectional hybrids, since sections *Dantia* and *Microcarpium* differ primarily in habit (creeping vs. erect with basal stolons) and phyllotaxy (opposite vs. alternate). The hybrids are listed below, with names of the parental species in section *Dantia* arbitrarily placed before those in section *Microcarpium*.

Ludwigia arcuata ($n = 16$) × *L. pilosa* Walter ($n = 16$)
Ludwigia palustris ($n = 8$) × *L. glandulosa* subsp. *glandulosa* ($n = 16$)

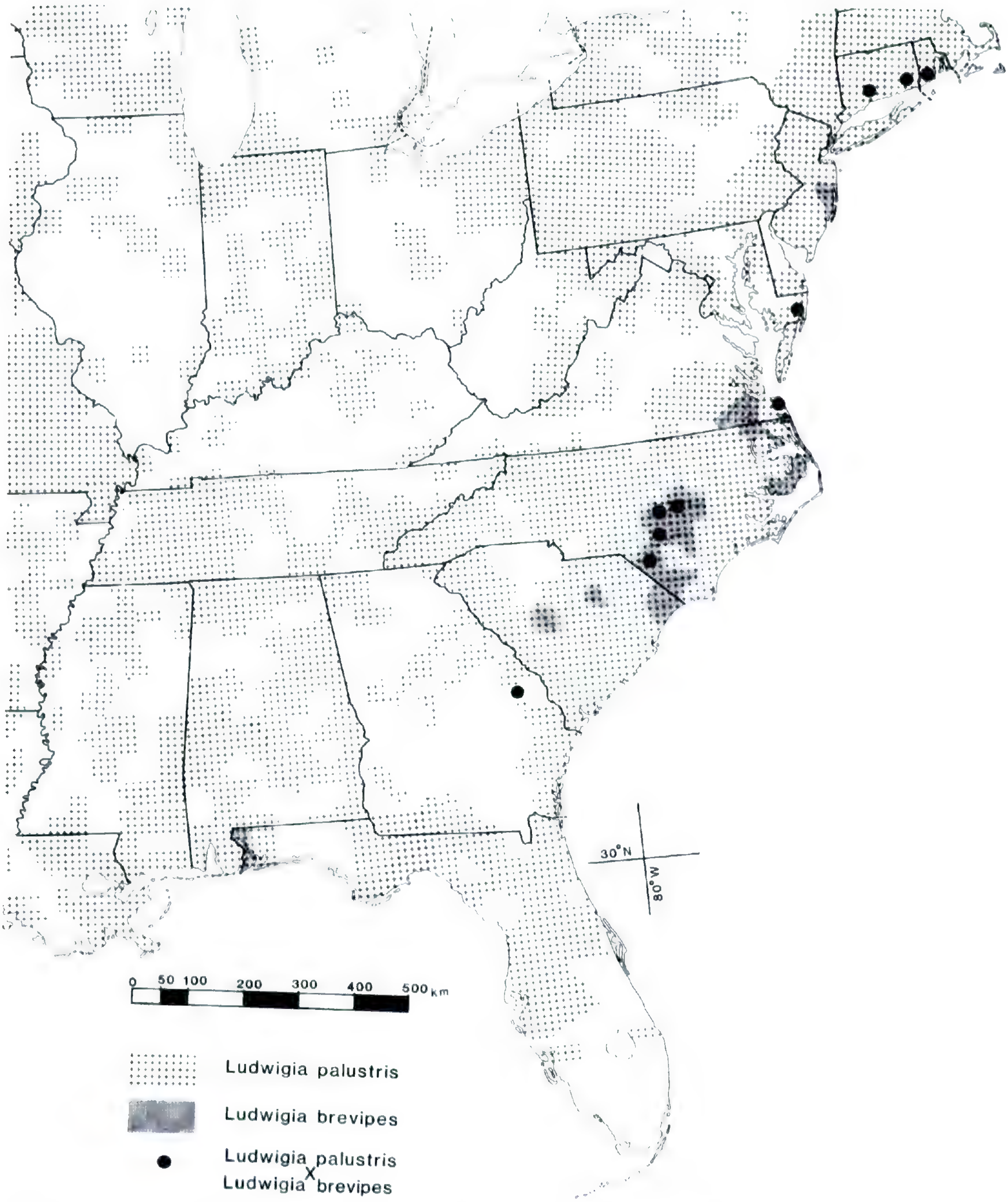

Figure 5. Distribution of the natural hybrids *Ludwigia brevipes* × *L. palustris* relative to the ranges of the putative parents (range of *L. palustris* is shown in part).

Ludwigia palustris ($n = 8$) × *L. microcarpa* Michx. ($n = 8$)
Ludwigia palustris ($n = 8$) × *L. polycarpa* Short & Peter ($n = 16$)
Ludwigia repens ($n = 24$) × *L. curtissii* Chapm. ($n = 32$)
Ludwigia repens ($n = 24$) × *L. simpsonii* Chapm. ($n = 24$)

Peng (1988) provided full voucher information and discussions for each of these hybrid combinations. Particularly in the case of species such as *L. curtissii* and *L. simpsonii*, Peng (1989) suggested that some diploid taxa in or ancestral to section *Dantia* may have been involved in their formation. The intersectional hybrids exhibited varying degrees of chromosome pairing in meiosis, suggesting moderate genetic compatibility between plants of the two North American sections. Although some

Table 4. Results of experimental hybridization program in *Ludwigia* sect. *Dantia*, including estimates of fruit set, seed set (actual and as a ratio of hybrid to selfed maternal seed), and pollen fertility in experimental F_1 hybrids. Pistillate parent listed first; vouchers for all parental species are listed in Table 3.

Species involved in hybridization	Fertile capsules set/pollination attempts (% fruit set)	Fertile seeds set per hybrid capsule (range) mean	Ratio of hybrid/selfed maternal seed set (as %)	Pollen grains examined in hybrid (% stainable)
L. palustris (2*x*) × *L. arcuata* (4*x*)	3/21 (14%)	(6–9) 8	7%	600 (3%)
L. palustris (2*x*) × *L. spathulata* (4*x*)	7/20 (35%)	(17–50) 35	32%	—
L. palustris (2*x*) × *L. brevipes* (6*x*)	10/24 (42%)	(11–61) 33	34%	600 (12%)
L. palustris (2*x*) × *L. repens* (6*x*)	8/21 (38%)	(19–108) 69	60%	800 (12%)
L. spathulata (4*x*) × *L. palustris* (2*x*)	11/16 (69%)	(17–61) 35	80%	400 (>1%)
L. spathulata (4*x*) × *L. arcuata* (4*x*)	5/26 (19%)	(2–4) 3	7%	1000 (25%)
L. spathulata (4*x*) × *L. brevipes* (6*x*)	6/19 (32%)	(1–18) 8	18%	500 (4%)
L. spathulata (4*x*) × *L. repens* (6*x*)	4/13 (31%)	(21–42) 33	75%	800 (17%)
L. arcuata (4*x*) × *L. palustris* (2*x*)	0/9 (0%)	—	0%	—
L. arcuata (4*x*) × *L. spathulata* (4*x*)	0/5 (0%)	—	0%	—
L. arcuata (4*x*) × *L. brevipes* (6*x*)	3/6 (50%)	(138–155) 146	37%	800 (83%)
L. arcuata (4*x*) × *L. repens* (6*x*)	7/10 (70%)	(14–57) 30	11%	1000 (60%)
L. brevipes (6*x*) × *L. palustris* (2*x*)	14/14 (100%)	(56–108) 84	58%	600 (4%)
L. brevipes (6*x*) × *L. arcuata* (4*x*)	8/8 (100%)	(66–192) 152	102%	800 (90%)
L. brevipes (6*x*) × *L. spathulata* (4*x*)	8/11 (73%)	(7–42) 22	15%	800 (7%)
L. brevipes (6*x*) × *L. repens* (6*x*)	6/7 (86%)	(6–135) 87	60%	1200 (93%)
L. repens (6*x*) × *L. palustris* (2*x*)	5/13 (38%)	(26–45) 35	49%	1200 (5%)
L. repens (6*x*) × *L. arcuata* (4*x*)	2/17 (12%)	(27–35) 31	44%	600 (54%)
L. repens (6*x*) × *L. spathulata* (4*x*)	4/21 (19%)	(18–53) 33	47%	600 (35%)
L. repens (6*x*) × *L. brevipes* (6*x*)	5/15 (33%)	(10–64) 41	58%	1200 (91%)

of these hybrids appear to persist well vegetatively, none set any viable seeds.

The natural intrasectional hybrids, such as *Ludwigia* ×*lacustris* (*L. palustris* × *L. brevipes*) and *L. arcuata* × *L. repens*, and some intersectional hybrids, such as *L. repens* × *L. simpsonii* and *L. palustris* × *L. glandulosa* (Peng 1988), grow with unusual vigor, sometimes even to the local exclusion of their progenitor species. Raven (1963b) and Boufford (1982) described an analogous example in the interspecific sterile hybrid *Circaea* ×*intermedia* (*C. lutetiana* L. × *C. alpina* L.), a widespread weed in Europe, even in parts of Ireland, e.g., where one of its parents is not found (Boufford, 1982).

Experimental Hybridization

Data from experimental hybridization are useful in determining chromosome homologies and relationships of the taxa concerned, demonstrating the presence or absence of genetic isolating mechanisms, and displaying at least some of the variation patterns generated by hybridization. Thus, we carried out an extensive hybridization program among all species of *Ludwigia* sect. *Dantia*. In order to avoid the possibility of self-pollination, which interferes with the artificial hybridization, we emasculated flower buds of all ovulate parents one day prior to opening. The stigmas were pollinated with fresh pollen of the hybridizing species the next day.

It takes one to two months for the capsules to mature. Since the mature capsules fall from the plants, it was necessary to inspect all plants daily. Seeds from the harvested capsules were counted and planted the following season. Populations of *Ludwigia* used in experimental hybridization are listed in Table 3. Twenty crosses in each direction between all possible pairs of species were attempted, although in some combinations there were too few flowers available to attempt this many crosses; Table 4 lists number of crosses attempted (range: 5 to 26) for each combination.

Fruit and Seed Set Following Experimental Hybridization

Most interspecific crosses resulted in at least some fruit set, ranging from 12% to 100% (Table 4). The only exception occurred in *L. arcuata*, with the largest flowers, when either of the apetalous, small-flowered species, *L. palustris* or *L. spathulata*, was the pollen donor. This parallels the situation in section *Microcarpium*, in which pollen of the smallest-flowered *L. microcarpa* consistently failed to fer-

tilize ovulate parents of large-flowered species with styles 3–6 times longer than those of *L. microcarpa* (Peng, 1988). In these cases, however, reciprocal crosses were successful.

Seed set in capsules formed as a result of interspecific crosses generally was lower than that observed in self-pollinated plants (Table 4), with one exception. The hybrid *L. brevipes* (6*x*) × *L. arcuata* (4*x*) (Fig. 13) on average set more seeds (152 seeds/capsule) than self-pollinated capsules of *L. brevipes* (146 seeds/capsule). The reciprocal cross, with *L. brevipes* as the pollen source, yielded the same average number of seeds as did self-pollinated *L. brevipes*, but much less than self-pollinated *L. arcuata* (253 seeds/capsule). In nature, however, the distributional ranges of these two species hardly overlap (Figs. 22, 24), and no natural hybrids are known. In fact, for all hybrid combinations involving *L. arcuata*, both fruit and seed set are reduced when *L. arcuata* is the pistillate parent compared to those where it is the staminate parent.

POLLEN FERTILITY IN HYBRIDS

We estimated pollen fertility in the hybrids as a percentage of stainable pollen, using cotton blue as a stain; the results appear in Table 4. Artificial hybrids tended to fall into two groups in terms of their fertility. In crosses involving *Ludwigia arcuata* (4*x*), *L. brevipes* (6*x*), and *L. repens* (6*x*), in all combinations and in reciprocal directions, the stainable pollen ranged from 54% to 93%, and these hybrids generally set more capsules with viable seeds than other hybrids. Hybrids involving the diploid *L. palustris* (2*x*) as staminate or pistillate parent with any other species produced very low pollen stainability (0%–12%), and those in all combinations with *L. spathulata* (4*x*) were only marginally more fertile (0%–35%); all capsules in hybrids involving *L. palustris* or *L. spathulata* aborted prior to seed maturation.

As noted above, some species of section *Dantia* shed their pollen in monads, others in tetrads. Hybrids between species that both shed pollen grains in monads also shed their grains in monads (with one sterile exception), and those between two tetrad-forming parents shed their pollen grains in tetrads (Table 5). Hybrids between a tetrad-former and a monad-former usually shed their pollen as monads. However, in all hybrids that produce fertile pollen involving *L. arcuata*, the species in which the pollen tetrads hold together most tightly, the pollen is shed in tetrads.

Table 5. Type of pollen release, as single grains (S) or tetrads (T), in parental species and their experimental F_1 hybrid progeny in *Ludwigia* sect. *Dantia*. Pistillate parent listed first; vouchers for all parental species are listed in Table 3.

Species involved in hybridization	Pollen type in F_1 progeny
L. palustris (S) × *L. arcuata* (T)	T
L. palustris (S) × *L. spathulata* (S)	hybrid pollen-sterile
L. palustris (S) × *L. brevipes* (T)	S
L. palustris (S) × *L. repens* (T)	S
L. spathulata (S) × *L. palustris* (S)	S
L. spathulata (S) × *L. arcuata* (T)	T
L. spathulata (S) × *L. brevipes* (T)	S
L. spathulata (S) × *L. repens* (T)	S
L. arcuata (T) × *L. palustris* (S)	no hybrids
L. arcuata (T) × *L. spathulata* (S)	no hybrids
L. arcuata (T) × *L. brevipes* (T)	T
L. arcuata (T) × *L. repens* (T)	T
L. brevipes (T) × *L. palustris* (S)	S
L. brevipes (T) × *L. arcuata* (T)	T
L. brevipes (T) × *L. spathulata* (S)	S
L. brevipes (T) × *L. repens* (T)	T
L. repens (T) × *L. palustris* (S)	S
L. repens (T) × *L. arcuata* (T)	T
L. repens (T) × *L. spathulata* (S)	S
L. repens (T) × *L. brevipes* (T)	T

MORPHOLOGY OF HYBRIDS

Artificial hybrids between members of section *Dantia* were easily produced and generally intermediate in morphology between their parents (compare Figs. 6–15 with Figs. 1–3). If one of the parents was pubescent and the other not, then the hybrid was pubescent, but usually not as densely as in the pubescent parent. Petioles, pedicels, sepals, and petals in the hybrids were intermediate in size between those of the parents. If one parent had petals and the other lacked petals, the hybrid usually possessed petals that were smaller than those of the petalous parent. Hybrids between the apetalous *L. spathulata* (4*x*) and small-petaled *L. repens* (6*x*) (Fig. 12), and those between the apetalous *L. palustris* (2*x*) and *L. repens* (Fig. 9) were exceptions in that they were often apetalous. Some hybrids had additional stamens in place of petals, in 1 to 4 of the normal petal positions. Such stamens were usually longer than the antesepalous ones, and in some instances possessed dilated, petaloid filaments. *Ludwigia palustris*, the only diploid species, has a green band on each of the four angles of its ovary wall that was not transmitted to the F_1 generation in any hybrid combination.

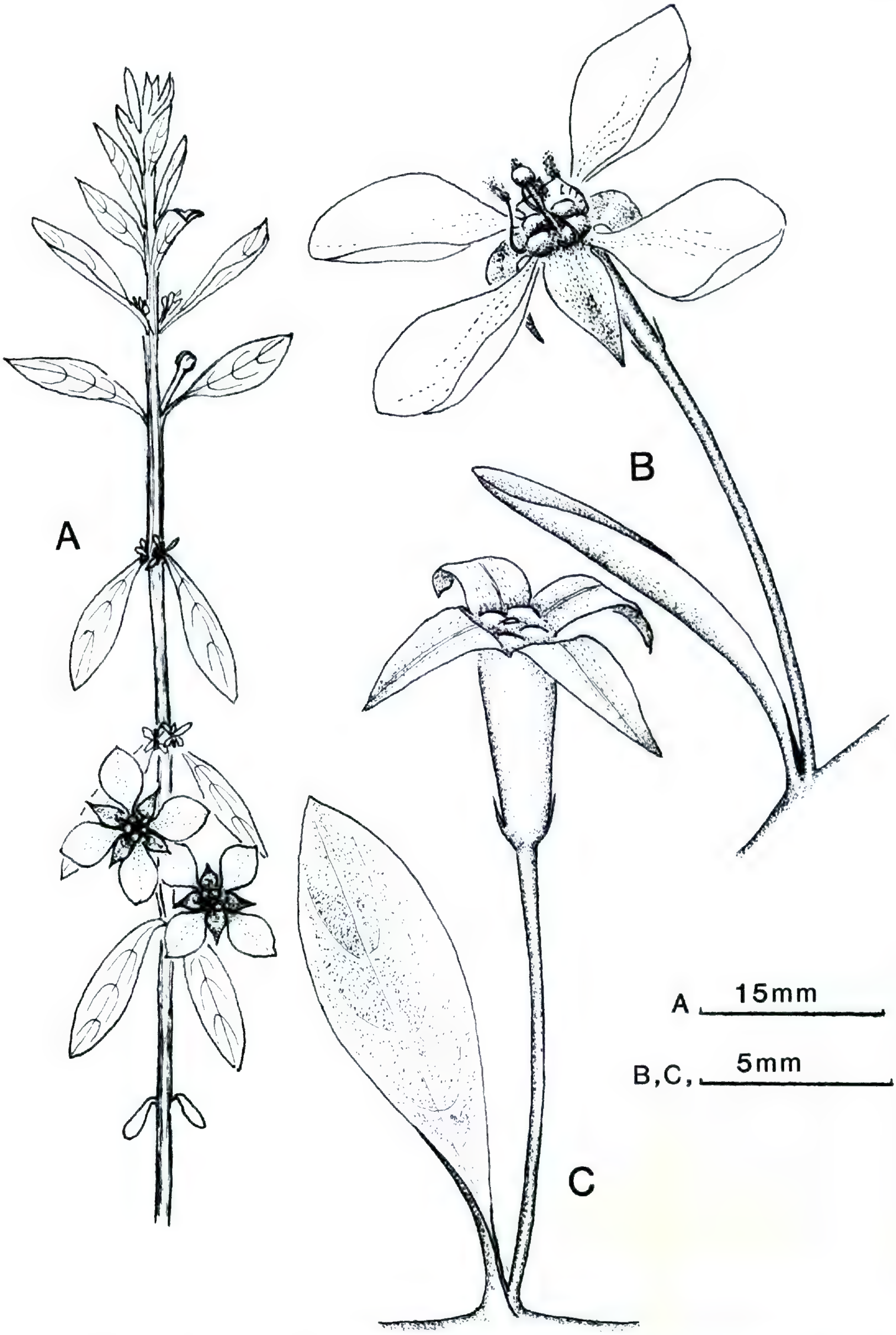

Figure 6. Experimental interspecific hybrid: *Ludwigia palustris* × *L. arcuata*. —A. Habit. —B. Flower. —C. Fruit. Parental vouchers: *L. palustris* (U.S.A. Arkansas, *Demaree 48955*, DS), *L. arcuata* (U.S.A. Florida, *Godfrey 62861*, DS).

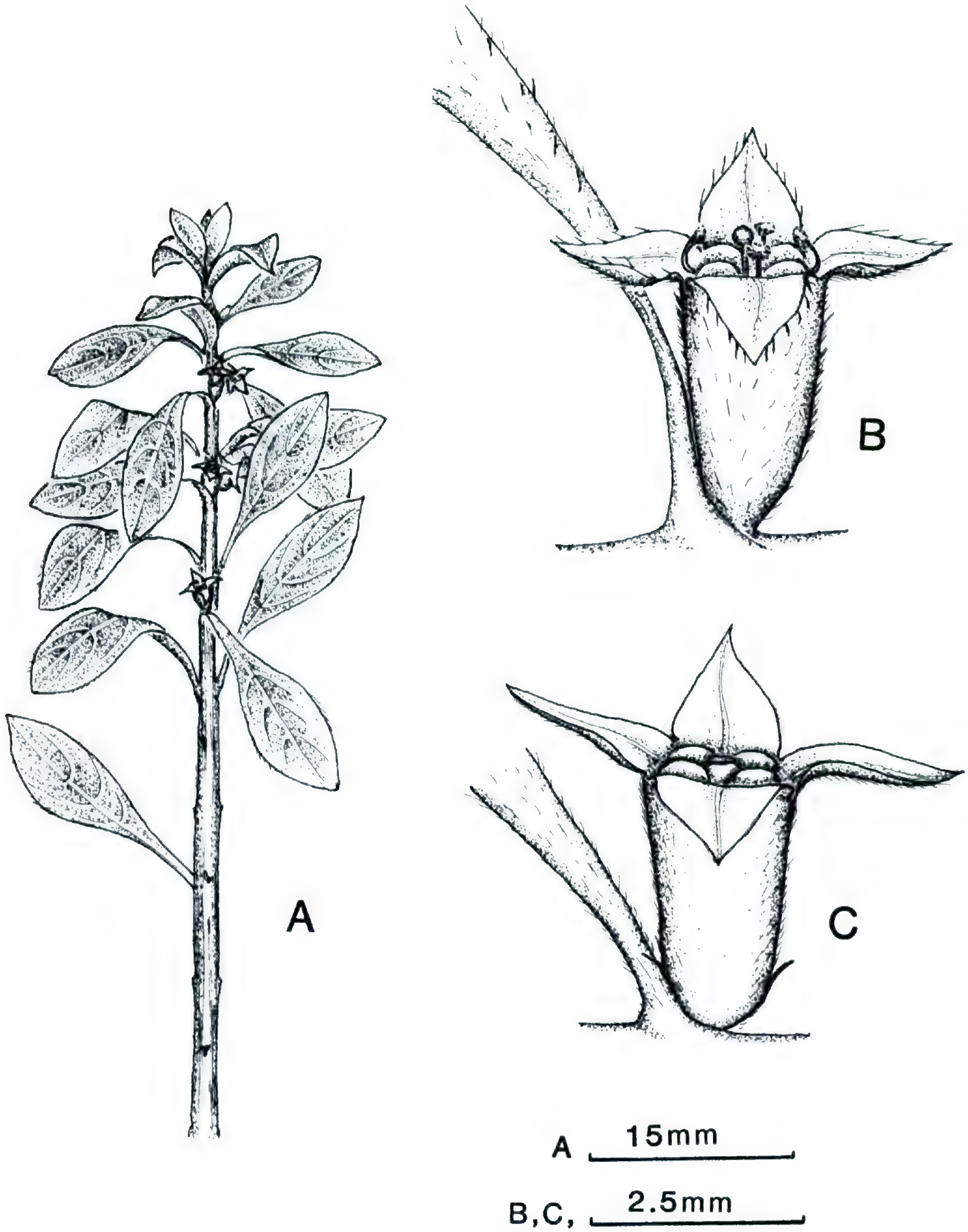

Figure 7. Experimental interspecific hybrid: *Ludwigia palustris* × *L. spathulata*. —A. Habit. —B. Flower. —C. Fruit. Parental vouchers: *L. palustris* (U.S.A. Arkansas, *Demaree 48955*, DS), *L. spathulata* (U.S.A. Florida, *Godfrey 62880*, DS).

A comparison of reciprocal crosses showed a slight tendency for maternal characteristics to dominate in all of the hybrids in section *Dantia*. This tendency was most noticeable in the shape and size of leaves and floral parts, particularly in hybrids between very distinct parents such as *Ludwigia palustris* and *L. brevipes*. In hybrids with *L. brevipes* as the pistillate parent, the petals were broadly elliptic (3–3.3 mm long, 2.1–2.2 mm wide). In hybrids with *L. palustris* as pistillate parent (Fig. 8), the petals were narrowly elliptic to elliptic (4–4.5 mm long, 1.7–1.8 mm wide). A similar tendency toward maternal inheritance of morphological characters is known in *Epilobium* (summary in Michael-

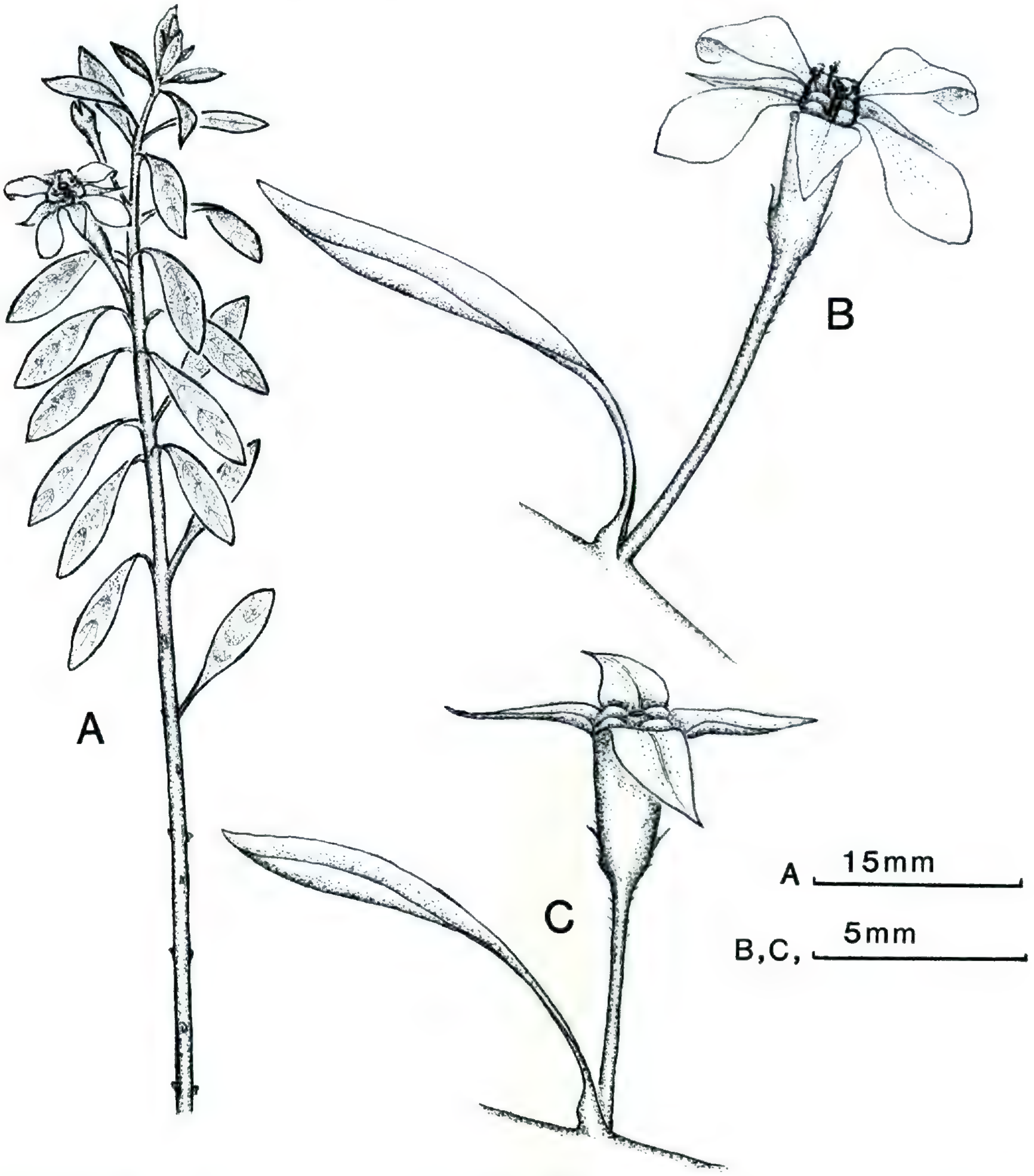

Figure 8. Experimental interspecific hybrid: *Ludwigia palustris* × *L. brevipes*. —A. Habit. —B. Flower. —C. Fruit. Parental vouchers: *L. palustris* (U.S.A. Arkansas, *Demaree 48955*, DS), *L. brevipes* (U.S.A. North Carolina, *Lloyd 1030*, DS).

is, 1965) and to a limited degree in *Circaea* (Boufford, 1982). Of the other genera of Onagraceae in which natural hybrids are known to occur and have been studied—including *Fuchsia* (Berry, 1982), *Gaura* (Carr et al., 1988), *Ludwigia* sect. *Microcarpium* (Peng, 1988), and *Oenothera* (Dietrich et al., 1997)—none has shown comparable reciprocal differences.

MEIOTIC ANALYSIS

As Stebbins (1950) pointed out, allopolyploidy is most likely to occur in a genus if its species can produce vigorous hybrids, yet remain sufficiently differentiated that most of their chromosomes cannot pair. *Ludwigia* sect. *Dantia* is a polyploid complex made up of one diploid (*L. palustris*), two tetraploid (*L. spathulata* and *L. arcuata*), and two hexaploid taxa (*L. repens* and *L. brevipes*). Many of the hybrids formed between species are vigorous and easily propagated vegetatively, which may increase the probability of polyploid changes through time.

In order to test for infraspecific variation, we made crosses between three populations of the

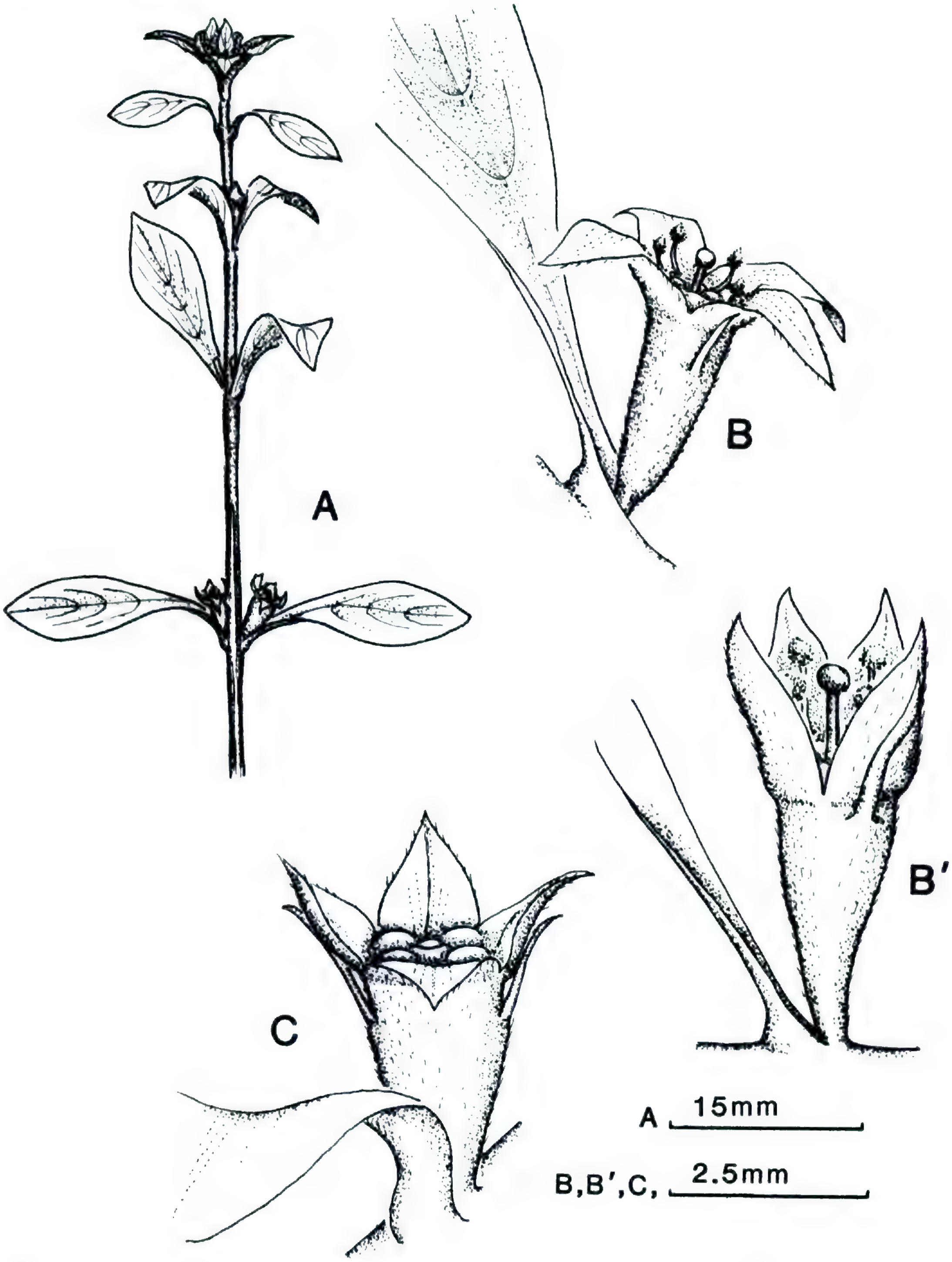

Figure 9. Experimental interspecific hybrid: *Ludwigia palustris* × *L. repens*. —A. Habit. —B., B′. Flower. —C. Fruit. Parental vouchers: *L. palustris* (U.S.A. Arkansas, *Demaree 48955*, DS), *L. repens* (U.S.A. Florida, *Raven 17932*, DS).

widespread and variable *Ludwigia repens* (Table 3), each with $n = 24$. Populations from Florida, California, and Nuevo León, Mexico (strains a–c, Table 3), were crossed in all combinations; the resulting hybrids regularly formed 24 pairs of chromosomes at meiotic metaphase I. Similarly, in the variable and widespread *L. palustris* ($n = 8$), crosses between populations from Arkansas, North Carolina,

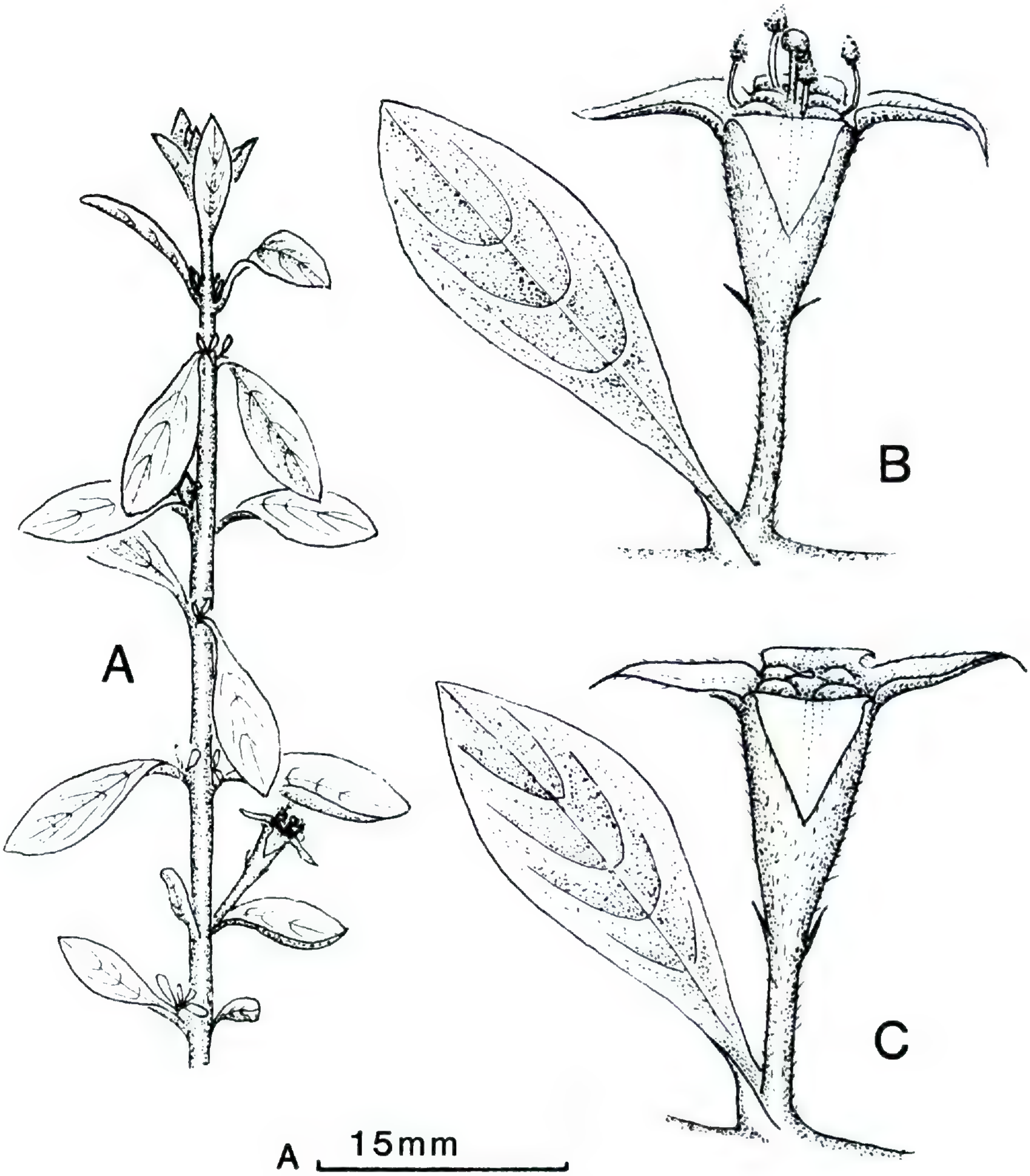

Figure 10. Experimental interspecific hybrid: *Ludwigia spathulata* × *L. arcuata*. —A. Habit. —B. Flower. —C. Fruit. Parental vouchers: *L. spathulata* (U.S.A. Florida, *Godfrey 62880*, DS), *L. arcuata* (U.S.A. Florida, *Godfrey 62861*, DS).

and California (strains a–c, Table 3) regularly formed eight pairs of chromosomes at meiotic metaphase I, like the parents.

Hybrids can be made between species of *Ludwigia* sect. *Dantia* in most combinations. Genomes of the species were assigned letter designations, with identity based on ability of a genome to form bivalents with another genome at meiotic metaphase I in hybrid plants. Arbitrarily, the diploid genome of *L. palustris* is designated AA. Artificial hybrids between *L. palustris* (2*x*) and *L. arcuata* (4*x*) form 24 univalents; therefore *L. arcuata* is designated as BBCC (Fig. 16). Because *L. repens* (6*x*) and *L. brevipes* (6*x*) form 24 bivalents when hybridized and have similar patterns of genome homology in the respective crosses with *L. arcuata* (4*x*) and *L. palustris* (2*x*), both of the hexaploids are designated AABBCC (see Fig. 16 for details). Although initial results (Schmidt, 1967) suggested that *L. spathulata* (4*x*) shared no genome homology with

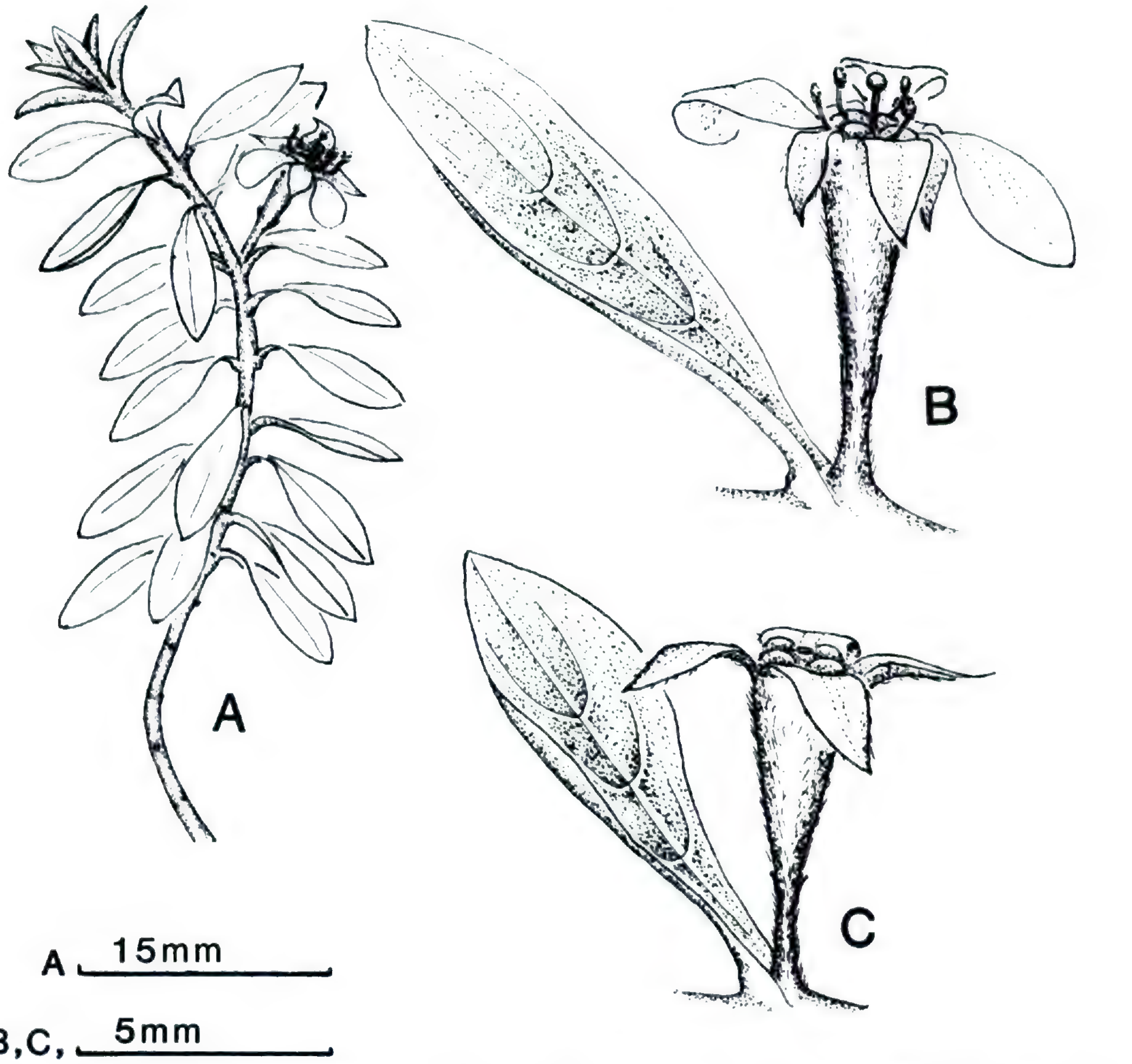

Figure 11. Experimental interspecific hybrid: *Ludwigia spathulata* × *L. brevipes*. —A. Habit. —B. Flower. —C. Fruit. Parental vouchers: *L. spathulata* (U.S.A. Florida, *Godfrey 62880*, DS), *L. brevipes* (U.S.A. North Carolina, *Lloyd 1030*, DS).

other species, we later found that it forms 8 bivalents and 8 univalents with *L. palustris* (2*x*) and 8 bivalents and 24 univalents with *L. repens* (6*x*), so *L. spathulata* is designated AADD, indicating that it contains a unique genome (DD) not shared with any other species of section *Dantia* (Fig. 16). *Ludwigia spathulata* (4*x*) is a rare species with the most limited distribution (Fig. 22) in the section and distinctive morphological features such as densely strigillose pubescence throughout the plant and dark reddish brown seeds; our cytological data suggest that it has distinctive genomic features as well.

No artificial hybrids were obtained in the crosses between *Ludwigia arcuata* and *L. spathulata*, nor were hybrids formed between *L. arcuata* and *L. palustris* when *L. arcuata* was the pistillate parent, although the reciprocal cross was successful. These results suggest that pollen from the short-styled species, *L. palustris* and *L. spathulata*, may be unable to grow down the length of the long styles of *L. arcuata* (with styles 3–10× the length of the smaller-flowered species; Table 2).

Ludwigia repens (6*x*) and *L. brevipes* (6*x*) are quite dissimilar morphologically, despite the fact that they share the same genomic complement (AABBCC). This suggests that these two species either had a common origin and subsequently diverged morphologically or had separate polyploid origins from species with similar genomic complements. *Ludwigia palustris* (AA) and *L. arcuata* (BBCC) could have given rise independently to both *L. repens* (AABBCC) and *L. brevipes* (AABBCC; Fig. 16) by hybridization followed by chromosomal doubling, possibly through the union of unreduced gametes. Since we found that artificial hybrids in this section frequently resemble the ma-

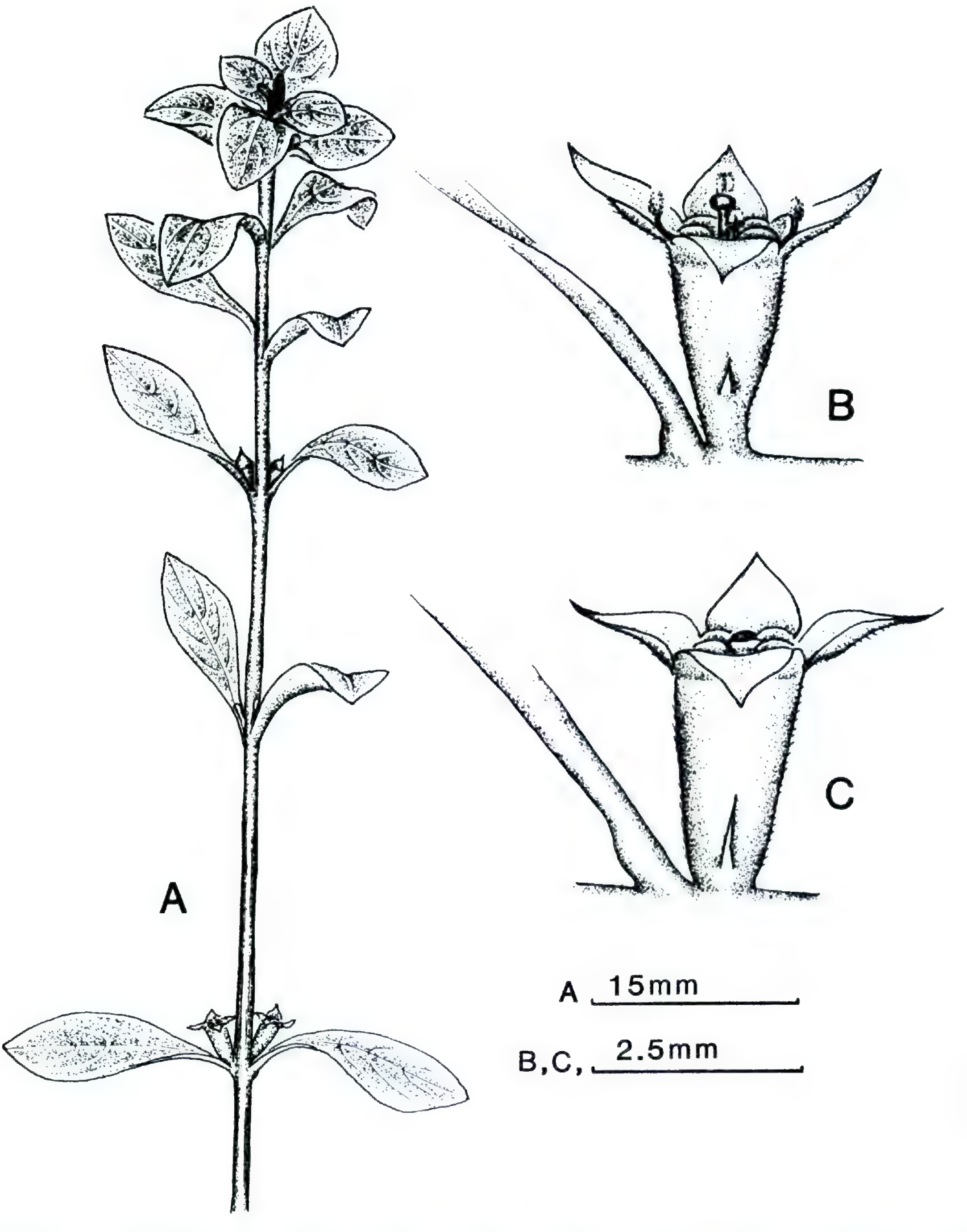

Figure 12. Experimental interspecific hybrid: *Ludwigia spathulata* × *L. repens*. —A. Habit. —B. Flower. —C. Fruit. Parental vouchers: *L. spathulata* (U.S.A. Florida, *Godfrey 62880*, DS), *L. repens* (U.S.A. Florida, *Raven 17932*, DS).

ternal parent in appearance, this at least suggests that the divergent morphology of the two hexaploids may reflect reciprocal origins from the same parental taxa. Alternatively, other species with similar complements, no longer extant, could have been the diploid/tetraploid progenitors.

The results of meiotic analysis of an experimental intersectional hybrid between *Ludwigia alternifolia* ($n = 8$; sect. *Ludwigia*: North Carolina, Carteret Co., *Broome 922*) and *L. repens* ($n = 24$; sect. *Dantia*; Florida, St. John's Co., *Dille 361*) suggest an alternative cytogenetic phylogeny for section *Dantia* (vouchers of hybrid and parents at MO). At meiotic metaphase I, this hybrid shows consider-

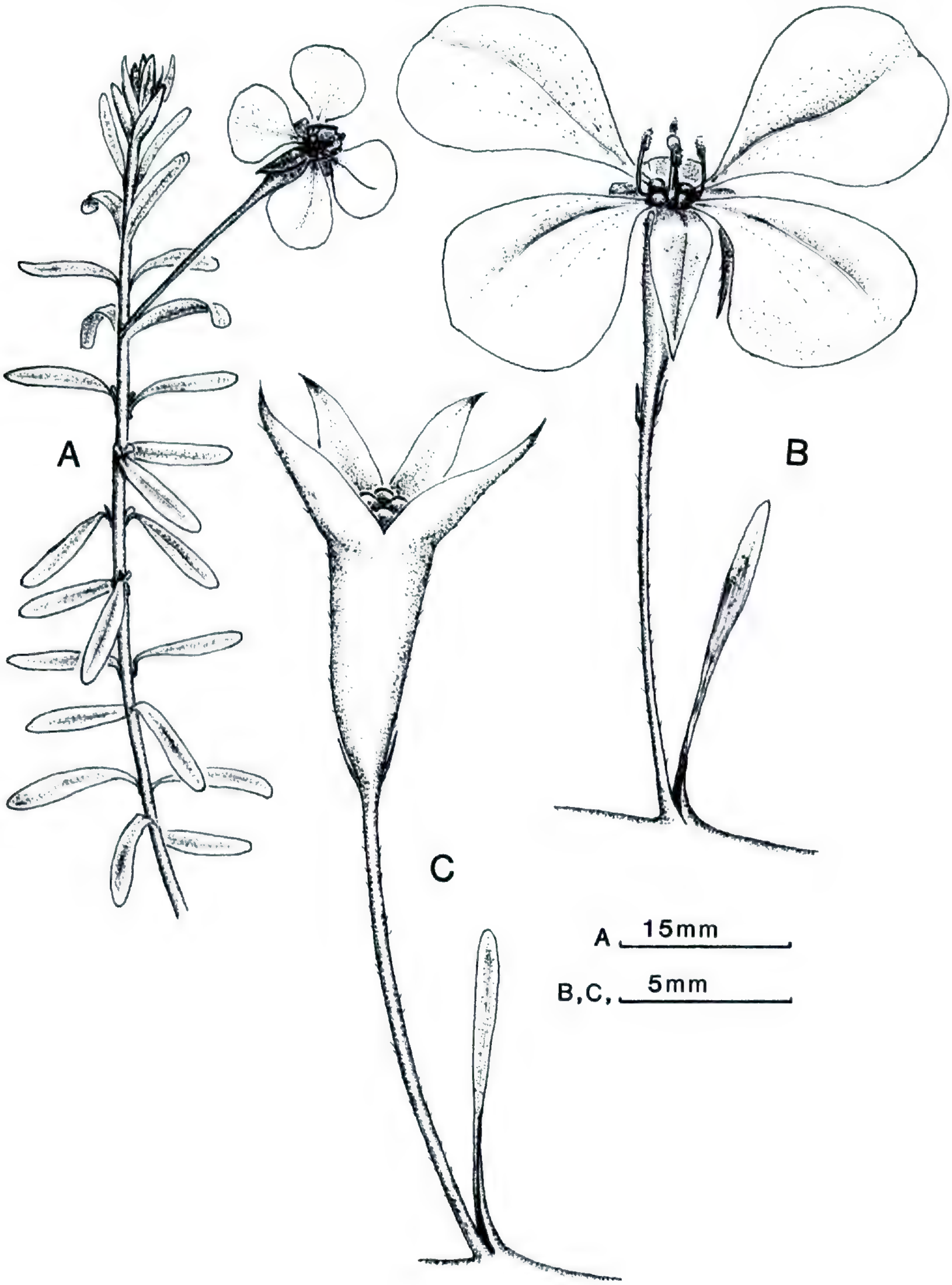

Figure 13. Experimental interspecific hybrid: *Ludwigia brevipes* × *L. arcuata*. —A. Habit. —B. Flower. —C. Fruit. Parental vouchers: *L. brevipes* (U.S.A. North Carolina, *Lloyd 1030*, DS), *L. arcuata* (U.S.A. Florida, *Godfrey 62861*, DS).

able variability, with different cells having 6 to 10 bivalents, 12 to 20 unpaired chromosomes, and an occasional trivalent, which suggests that the parents may share a pairable genome. Section *Ludwigia* differs fundamentally from section *Dantia*: species in the former section are erect perennial herbs with tuberous roots, alternate leaves, nectaries with four shallow ciliate depressions on the raised summit of the ovary, and capsules dehiscing by a terminal pore formed after abscission of the style base (Raven, 1963a; Munz, 1965; Lutz, 1986). Because both sections occur mainly in eastern

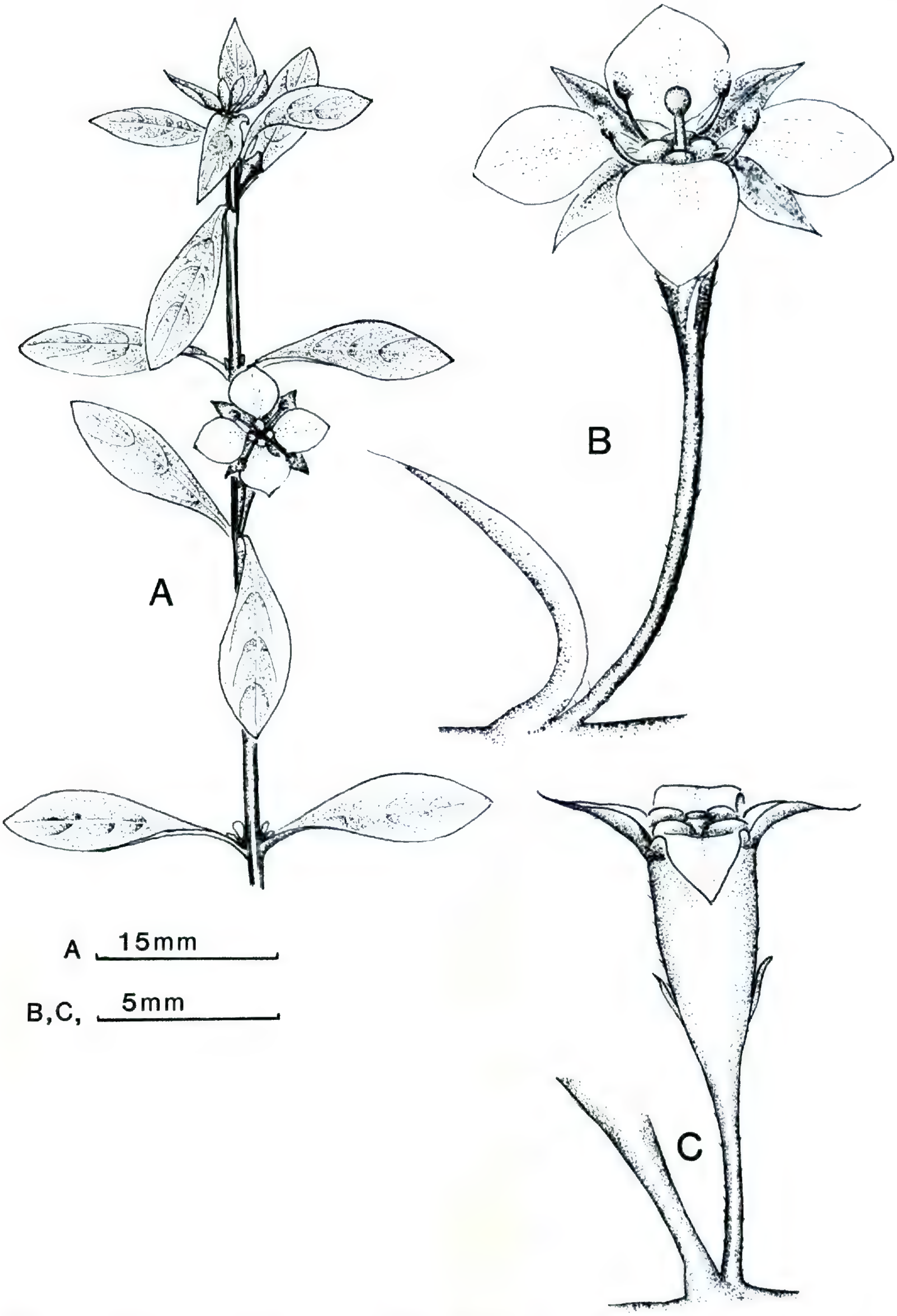

Figure 14. Experimental interspecific hybrid: *Ludwigia arcuata* × *L. repens*. —A. Habit. —B. Flower. —C. Fruit. Parental vouchers: *L. arcuata* (U.S.A. Florida, *Godfrey 62861*, DS), *L. repens* (U.S.A. Florida, *Raven 17932*, DS).

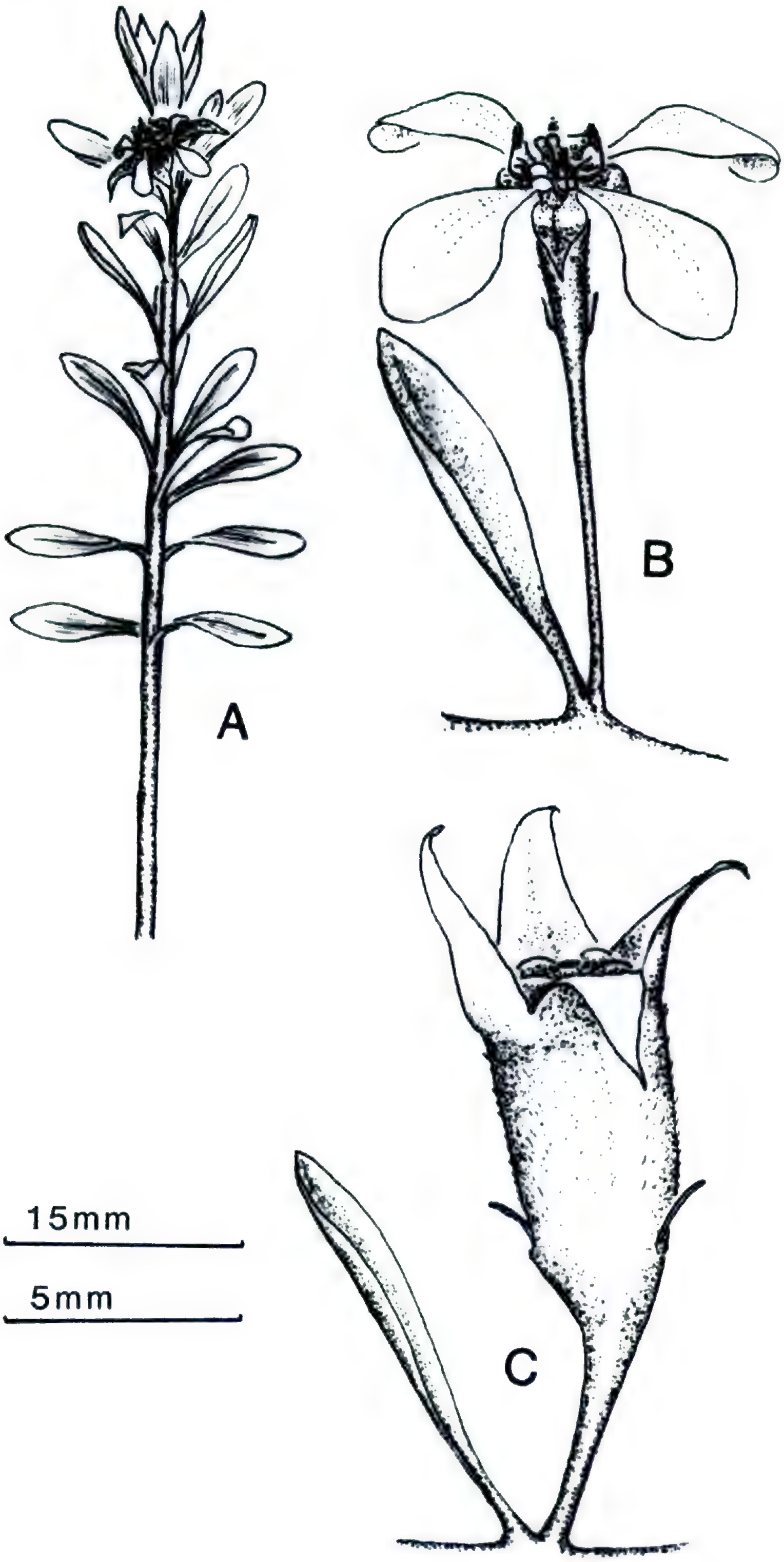

Figure 15. Experimental interspecific hybrid: *Ludwigia brevipes* × *L. repens*. —A. Habit. —B. Flower. —C. Fruit. Parental vouchers: *L. brevipes* (U.S.A. North Carolina, *Lloyd 1030*, DS), *L. repens* (U.S.A. Florida, *Raven 17932*, DS).

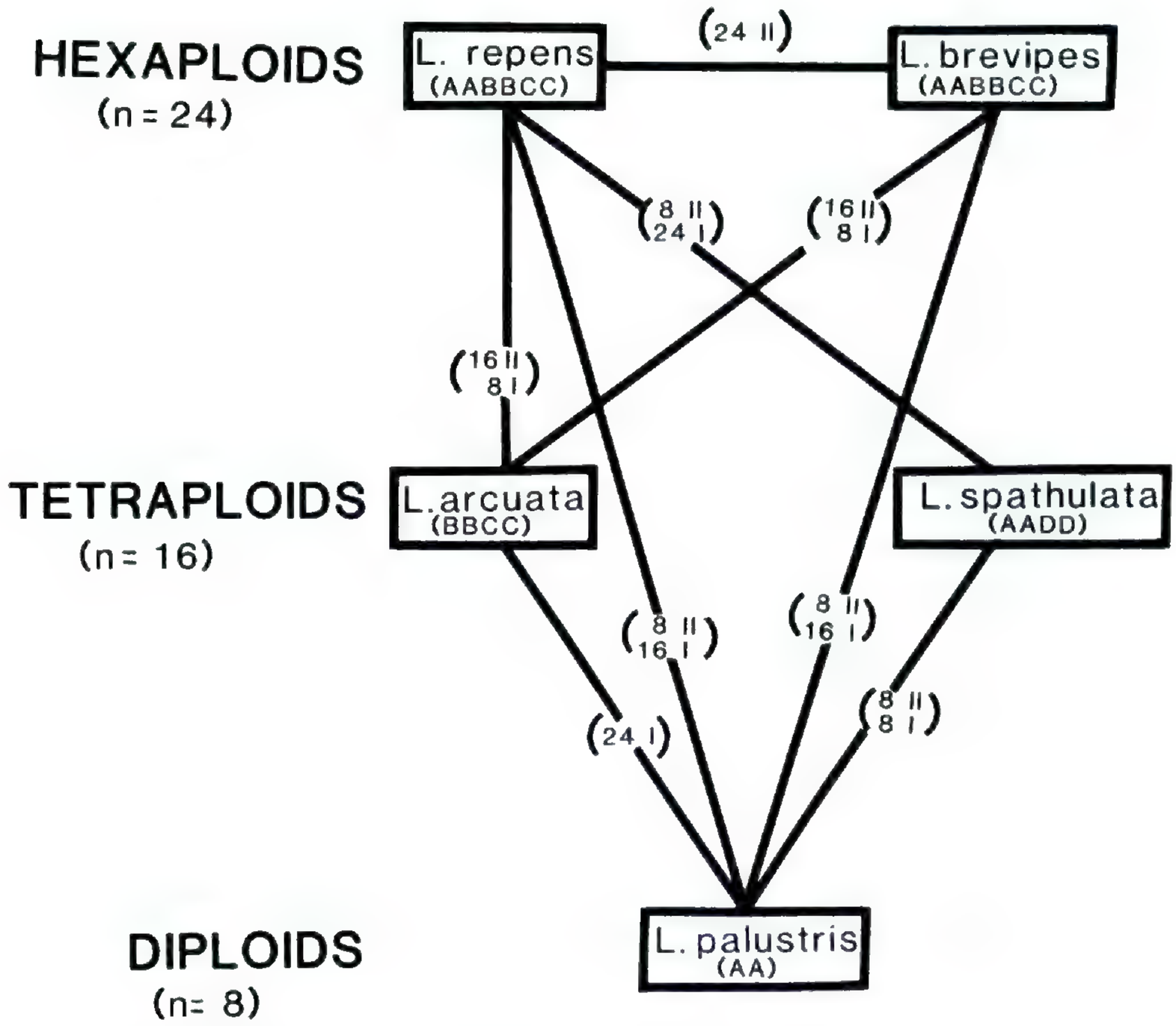

Figure 16. Genomic relationships based on chromosome pairing at meiotic metaphase I in interspecific hybrids, and presumed phylogenetic relationships among species in *Ludwigia* sect. *Dantia*.

North America and share such features as pluriseriate seeds, 4-merous flowers, and stamens as many as sepals, they often have been considered closely related (Raven, 1963a; Munz, 1965). However, some of these character states may be plesiomorphic (Eyde, 1981), and this relationship needs clarification. Although it is possible that the observed bivalent formation might involve a genome shared between *L. alternifolia* and *L. repens*, it seems unlikely, given the apparent phyletic distance between the respective sections.

As an alternative explanation, the bivalents formed in this intersectional hybrid may result from pairing between two of the three genomic complements in the hexaploid *L. repens* (e.g., AA with CC), rather than involving the genome of the second species. If true, this suggests an alternative interpretation (Fig. 17) of the genomic relationships among species of section *Dantia*, differing from Figure 16 mainly by suggesting that the diploid *L. palustris* did not participate in the formation of the hexaploids *L. repens* or *L. brevipes*. In this alternative, the bivalents observed in hybrids between *L. palustris* and either hexaploid result from pairing between two of the three genomes present in the hexaploid parent, rather than between genomes of that taxon and *L. palustris*. However, the close resemblance between *L. brevipes* (Fig. 25) and the experimental hybrid *L. arcuata* × *L. palustris* (Fig. 6) challenges the notion that the genome of *L. palustris* is completely unrelated to that of *L. brevipes*. Also, the chromosome pairings (8 II) in *L. palustris* × *L. repens* are very consistent, unlike those of *L. alternifolia* × *L. repens* (6–10 II). We favor, therefore, the earlier scheme (Fig. 16), which suggests that *L. palustris* contributed its AA genome to the formation of the hexaploid *L. repens*. A more complete understanding of the chromosome pairings observed between *L. repens* and *L. alternifolia* and of the possible relationship between sections *Dantia* and *Ludwigia* is the focus of an ongoing molecular systematic analysis.

Systematic Treatment

We here adopt a pragmatic approach to defining the species units, essentially in keeping with criteria adopted throughout the Onagraceae, articulated first in *Clarkia* by Lewis and Lewis (1955) and restated by Raven (1976b, 1980). Species are defined by morphological discontinuities in two or more characters, in this case further supported by differences in ploidy level among most taxa. As detailed in this report, the species of *Ludwigia* sect. *Dantia* occur in various combinations of sympatry and are capable of hybridizing, in some cases producing quite fertile offspring. Despite this, most populations can be diagnosed easily as one or an-

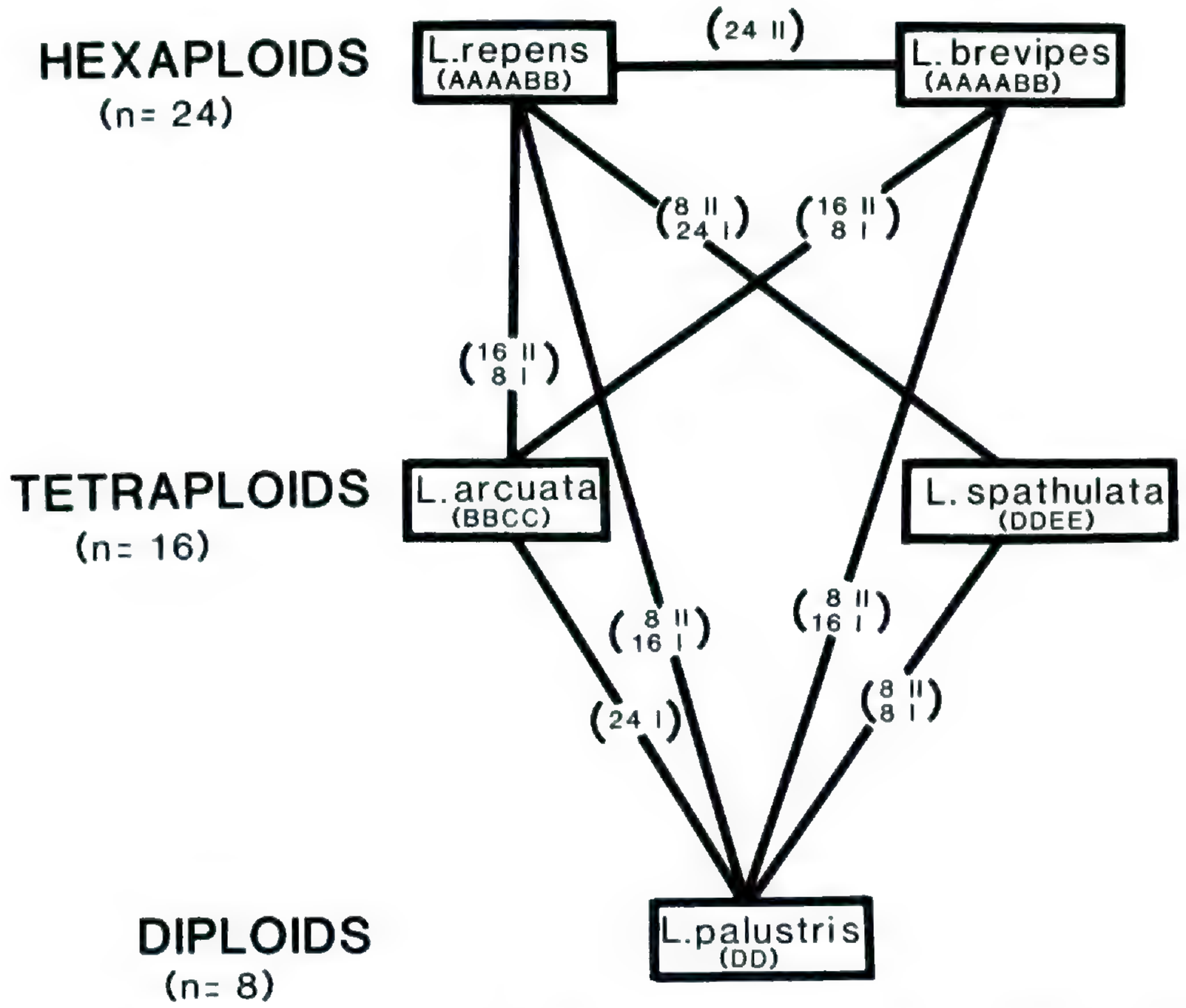

Figure 17. Alternative scheme for genomic relationships based on chromosome pairing in *Ludwigia* sect. *Dantia*; compare to Figure 16.

other species by combinations of several morphological characters. We do not recognize infraspecific taxa in any species of this section.

For this study, we examined more than 3000 herbarium specimens during 1986–1992, several hundred new field collections by Peng during the same period, and multiple accessions of all species cultivated from seed or field-collected plants at Stanford in 1963–1967 by Raven and Schmidt, and at St. Louis in 1986–1992 by Peng. For the sake of brevity, we have cited only a selection of these specimens, especially under *Ludwigia palustris*, where we cite only one collection per state in the United States, usually that with the widest herbarium distribution. We have attempted to maintain comparable coverage outside of the United States.

Ludwigia L., Sp. Pl. 1: 118 (as *Ludvigia*), 1204. 1 May 1753. TYPE: *Ludwigia alternifolia* L. (lectotype, designated by Britton & A. Brown (1913: 586)).

Isnardia L., Sp. Pl. 1: 120. 1753. *Ludwigia* sect. *Isnardia* (L.) Torr. & A. Gray, Fl. N. Amer. 1: 525. 1840. TYPE: *Isnardia palustris* L. [= *Ludwigia palustris* (L.) Elliott].

[See Raven (1963a) for complete generic synonymy.]

Perennial (rarely annual) herbs, shrubs or small trees; stems usually well-branched, erect or creeping and rooting at the nodes, sometimes floating; submerged stems often swollen and spongy, sometimes with spongy pneumatophores. Leaves alternate or opposite, rarely whorled, simple, mostly entire; stipules present in at least upper part of stem, often deciduous, deltoid. Flowers diurnal, in spicate inflorescence or single and axillary, radial, 3- to 7-merous; hypanthium lacking; usually with 2 bracteoles at base of ovary; sepals persistent after anthesis; petals as many as sepals or absent, caducous, yellow or white; stamens as many as or twice as many as sepals; anthers versatile or basifixed by reduction; pollen shed singly or in tetrads or polyads; ovary with as many locules as sepals; disc (summit of ovary) flat to conical, often with depressed or raised nectaries at bases of epipetalous stamens; stigma capitate or hemispheric, often lobed; placentation axile; ovules pluriseriate or uniseriate in each locule (rarely mixed). Capsules dry, dehiscing from a terminal pore, or by flaps separating from valve-like top, or irregularly. Seeds rounded or elongate; pluriseriate seeds naked, usually with evident raphe, uniseriate seeds usually embedded in powdery or woody endocarp from which they detach easily or with difficulty.

The authority for lectotypification of *Ludwigia* is obscure, although this clearly was accomplished for the first time in Britton and Brown (1913). Britton was primary author of the entire work (Brown being

only honorary; Stafleu & Cowan, 1976: 334), but he noted on the Onagraceae treatment (p. 584): "Text revised with the assistance of Dr. John K. Small." In the first edition (Britton & Brown, 1897: 475), the footnote read simply: "Text revised by Dr. John K. Small." The rather eclectic family treatment in both editions conforms closely with the treatments found in Small (1897, 1903, 1933), for example recognizing *Ludwigiantha* at the generic level, which suggests that Small may in fact have been the primary author for the treatment of the Onagraceae. However, because (1) no authority is specified, (2) despite those footnotes Small is not credited as primary author, and (3) the text does not specifically credit Britton as primary author of the *Flora*, we have ascribed lectotypification to Britton and Brown (1913).

Ludwigia sect. **Dantia** (DC.) Munz, Bull. Torrey Bot. Club 71: 153. 1944. *Isnardia* sect. *Dantia* DC., Prodr. 3: 61. 1828. TYPE: *Ludwigia palustris* (L.) Elliott.

Isnardia sect. *Ludwigiaria* DC., Prodr. 3: 60. 1828. TYPE: *Isnardia pedunculosa* (Michx.) DC. [= *Ludwigia arcuata*] (lectotype, designated here).

Ludwigia sect. *Ludwigiantha* Torr. & A. Gray, Fl. N. Amer. 1: 526. 1840. *Ludwigiantha* (Torr. & A. Gray) Small, Bull. Torrey Bot. Club 24: 178. 1897. TYPE: *Ludwigia arcuata* Walter.

Perennial herbs; stems creeping with ascending tips, rooting at nodes, the roots fibrous. Stems usually well-branched and forming mats, never becoming swollen and spongy when entirely submerged. Leaves opposite, green, often flushed red with age, entire, usually with hydathodal glands along margins. Flowers 4-merous, axillary, sessile to long-pedicellate; bracteoles in subopposite pairs attached from the pedicel to halfway up the ovary; sepals greenish or yellowish green; petals present or absent; stamens 4 in a single whorl, antesepalous; anthers introrse; pollen shed singly or as loose or tight tetrads; nectary disc quadrangular, inconspicuously to distinctly 4-lobed and elevated above ovary summit; stigma glabrous, subglobose. Capsules 4-loculed, with ca. 45 to 250 seeds, oblong-ovoid to oblong-obovoid, elongate obpyramidal, or clavate, tardily dehiscent. Seeds yellowish to light tan or reddish brown, free and pluriseriate in each locule, with a narrow raphe; surface cells columnar, transversely elongate to the seed length. Self-compatible. Gametic chromosome number, $n = 8, 16, 24$.

Distribution. The species of section *Dantia* primarily occur on the Atlantic and Gulf Coastal Plain of the United States; several of them occur more widely. *Ludwigia repens* also occurs in southwestern North America and adjacent northern Mexico, in the Caribbean Islands, and sporadically naturalized in Bangladesh (Khan, 1977) and Japan (Murata & Peng, 1988). *Ludwigia palustris* is widespread in temperate North America, extending through the Caribbean region and Central America to Colombia in South America, and also in temperate Eurasia, extending to northern Africa and now introduced in southern Africa and the Pacific-Australasian region.

The original use of the name *Dantia*, cited in synonymy by Linnaeus in *Species Plantarum* (1753) and in *Genera Plantarum* (1737), was by F. P. Du Petit, who in 1710 described *Dantia palustris* in *Lettres d'un Medecin*. While noting Du Petit's generic name (referenced as "*Petit.* gen."), Linnaeus (1753) chose not to use it, instead describing his genus as *Isnardia*. Curiously, both epithets commemorate Antoine-Tristan Danty d'Isnard (1663–1743). In describing his section *Dantia*, Candolle (1828) credited this earlier use of the name incorrectly to "Du Pet.-Thouar. Gen.," which refers to L. M. A. Petit-Thouars's *Genera Nova Madagascariensia* (1806); this error was noted by Des Moul (Actes Soc. Linn. Bordeaux 10: 516–518. 1860). Several authors subsequent to Linnaeus illegitimately described genera based on the same type (*Isnardia palustris*), including: *Dantia* Boehm. in Ludw., Def. Gen. Pl. ed. 3. 388. 1760, nom. illeg.; *Tiphogeton* Ehrh., Beitr. 4: 146. 1789, nom. illeg.; *Danthia* Steud., Nom. Bot. ed. 2, 1: 482. 1840, nom. illeg.; *Quadricosta* Dulac, Fl. Hautes-Pyrénées 329. 1867, nom. illeg.

In his *Prodromus*, Candolle (1828) also recognized *Ludwigia*, but modified Linnaeus's (1753) concept of the genus, removing *L. alternifolia* (lectotype of the genus) to *Isnardia* and questioningly retaining *L. perennis* as "species vix notae." Within *Isnardia*, Candolle distinguished species with petals as section *Ludwigiaria*, including *L. alternifolia*, several species now included in section *Microcarpium*, and two species now treated in section *Dantia*. We have selected one of the latter, *Isnardia pedunculosa* (= *L. arcuata*), as the type of Candolle's section *Ludwigiaria* in order to retain an element of Linnaeus's original conception of *Isnardia*.

KEY TO THE SPECIES OF *LUDWIGIA* SECT. *DANTIA* WORLDWIDE

1a. Petals absent; sepals 1–1.7 mm long; anthers 0.2–0.4 mm long; pollen shed as monads.

2a. Plants nearly glabrous; seeds yellowish brown . . . . . 1. *L. palustris*
2b. Plants densely strigillose throughout; seeds dark reddish brown . . . . . 2. *L. spathulata*

1b. Petals 4, caducous; sepals 1.8–10 mm long; anthers 0.4–2 mm long; pollen shed as tight or loose tetrads.
3a. Leaves narrowly to broadly elliptic; petals 1–3 mm long; sepals 1.8–4 mm long, about as long as wide; mature pedicels 0–3.5(–5) mm long . . . . . 5. *L. repens*
3b. Leaves narrowly elliptic or oblanceolate elliptic to linear; petals 4–11 mm long; sepals 4–10 mm long, about 2–3 times as long as wide; mature pedicels (4.5–)6–45 mm long.
4a. Petals 4–5 mm long; anthers 0.75–1 mm long; pedicels of capsules as long as or shorter than subtending leaves . . . . . 4. *L. brevipes*
4b. Petals 7–11 mm long; anthers 1.3–2 mm long; pedicels of capsules usually much longer than subtending leaves . . . . . 3. *L. arcuata*

1. Ludwigia palustris (L.) Elliott, Sketch Bot. S. C. & Ga. 1: 211. 1817. *Isnardia palustris* L., Sp. Pl. 1: 120. 1753. *Ludwigia palustris* var. *typica* Fernald & Grisc., Rhodora 37: 176. 1935. TYPE: Presumably from Europe, collector unknown (lectotype, LINN 157.3 not seen; designated by Raven in Jarvis et al. (Regnum Veg. 127: 57. 1993); microfiche!). Figures 1–3, 18.

Ludwigia apetala Walter, Fl. Carol. 89. 1788. TYPE: U.S.A. South Carolina, vicinity of Berkeley Co., 1768–1788, *T. Walter s.n.* (holotype, *Walter Herbarium 66* upper left-hand specimen, BM not seen; microfiche!)

Ludwigia nitida Michx., Fl. Bor.-Amer. 1: 87. 1803. *Isnardia nitida* (Michx.) Poir., in Lam., Encyc. Suppl. 3: 188. 1813. TYPE: U.S.A. "In moist places, lower Carolina" [probably South Carolina], May, *A. Michaux s.n.* (holotype, P not seen, photo of holotype at GH!, MO!; probable isotypes, P!, PH!).

Isnardia palustris L. β *americana* DC., Prodr. 3: 61. 1828. *Ludwigia palustris* (L.) Elliott var. *americana* (DC.) Fern. & Griscom, Rhodora 37: 176. 1935. TYPE: U.S.A. "Carolina," *Bosc s.n.* (lectotype, designated by Raven (1963a: 400), G-DC not seen; microfiche!).

Isnardia ascendens J. Hall, in Eaton, Man. Bot. N. Amer. ed. 7. 353. 1836. TYPE: U.S.A. New York: Albany Co., Albany (type, F not seen).

Isnardia palustris L. f. *submersa* Glück, Biol. & Morphol. Unters. Wasser Sumpfgewachse 3: 155. 1911. *Ludwigia palustris* (L.) Elliott f. *submersa* (Glück) Eames, Rhodora 35: 229. 1933. *Ludwigia palustris* (L.) Elliott var. *americana* (DC.) Fern. & Grisc. f. *elongata* Fassett, Rhodora 41: 377. 1939, nom. illeg. subst. TYPE: France. Landes, "from a pond near Dax," s.d., s. col. (lectotype, designated here, Glück, Biol. & Morphol. Unters. Wasser Sumpfgewachse 3: tafel IV, fig. 21a. 1911).

Ludwigia palustris (L.) Elliott var. *liebmannii* [as "liebmanni"] H. Lév., Bull. Acad. Int. Géogr. Bot. 22: 24. 1912. TYPE: Mexico. Mont Frasu, 3000 m, s.d., *F. M. Liebmann s.n.* (holotype, C!; isotype, GH!).

Ludwigia palustris (L.) Elliott var. *inundata* Svenson, Torreya 35: 120. 1935. TYPE: U.S.A. New York: Dutchess Co., tidal mud of Stony Creek, Red Hook, 11 Oct. 1934, *M. Elwert & H. Svenson 6446* (holotype, NY!; isotypes, CAS!, F!, GH [2]!, MO!, US!, WISC!).

Ludwigia palustris (L.) Elliott var. *pacifica* Fern. & Griscom, Rhodora 37: 176. 1935. TYPE: Canada. British Columbia: Vancouver Island, gravelly shore (sand, mud, & gravel), Sproat Lake, 14 July 1914, *W. R. Carter 128* (holotype, GH!).

Ludwigia palustris (L.) Elliott var. *nana* Fern. & Griscom, Rhodora 37: 176. 1935. TYPE: U.S.A. Louisiana: Cameron Parish, 5 July 1903, *S. M. Tracy 8718* (holotype, GH!; isotypes, F!, MO!, MSC!, NO!, NY!, PH!, TAES!, US!).

Perennial herbs with prostrate or ascending stems, rooting at the nodes, up to 50 cm or longer, well-branched and forming mats. Leaves narrowly to broadly elliptic or ovate-elliptic, the blades 5.5–45 × 2.5–23 mm, glabrous, apex subacute, margin entire and minutely strigillose, the hairs 0.05–0.1 mm long, base abruptly attenuated into narrowly winged petioles 1.2–25 mm long; stipules minute, reddish purple, lanceolate to ovate-deltate, 0.15–0.25 × 0.05–0.15 mm, succulent; bracteoles minute, ± linear, 0.25–1(–1.8) × 0.05–0.8 mm, flanking ovary base or attached up to 2.5 mm above base, sometimes on very short pedicels. Flowers axillary and usually paired; sepals green, ovate-deltate, 1.1–2 × 1–2.1 mm, ascending, glabrous, apex acuminate, sometimes with a blunt tip, margin finely serrulate and minutely strigillose, the hairs 0.02–0.05 mm long; petals absent; anthers 0.2–0.4 × 0.3–0.6 mm; filaments translucent, 0.4–0.6 mm long; pollen shed singly; nectary disc green, elevated 0.15–0.3 mm on ovary apex, 1–2 mm across, 4-lobed, glabrous; style pale green, 0.35–0.7 mm long, glabrous; stigma whitish, subglobose, 0.2–0.4 mm across. Capsules dull light brown, oblong-obovoid or oblong with abruptly constricted base, (1.6–)2–5 mm long, 1.5–3(–3.5) mm thick, obscurely 4-angled, with a green, longitudinal band 0.4–1 mm wide on the central part of each side of the capsule, representing the thinnest part of the fruit wall, minutely strigillose, the hairs ca. 0.05 mm long, subsessile or with pedicels up to 0.5 mm long. Seeds yellowish brown, ellipsoid, 0.5–0.7 × 0.3–0.35 mm, the surface cells transversely elongate. Self-compatible. Gametic chromosome number, $n = 8$.

Phenology. Flowering and fruiting period: February to October.

Distribution (Figs. 19, 20). *Ludwigia palustris* is widespread in North America, along the eastern seaboard from Newfoundland and Quebec, Canada,

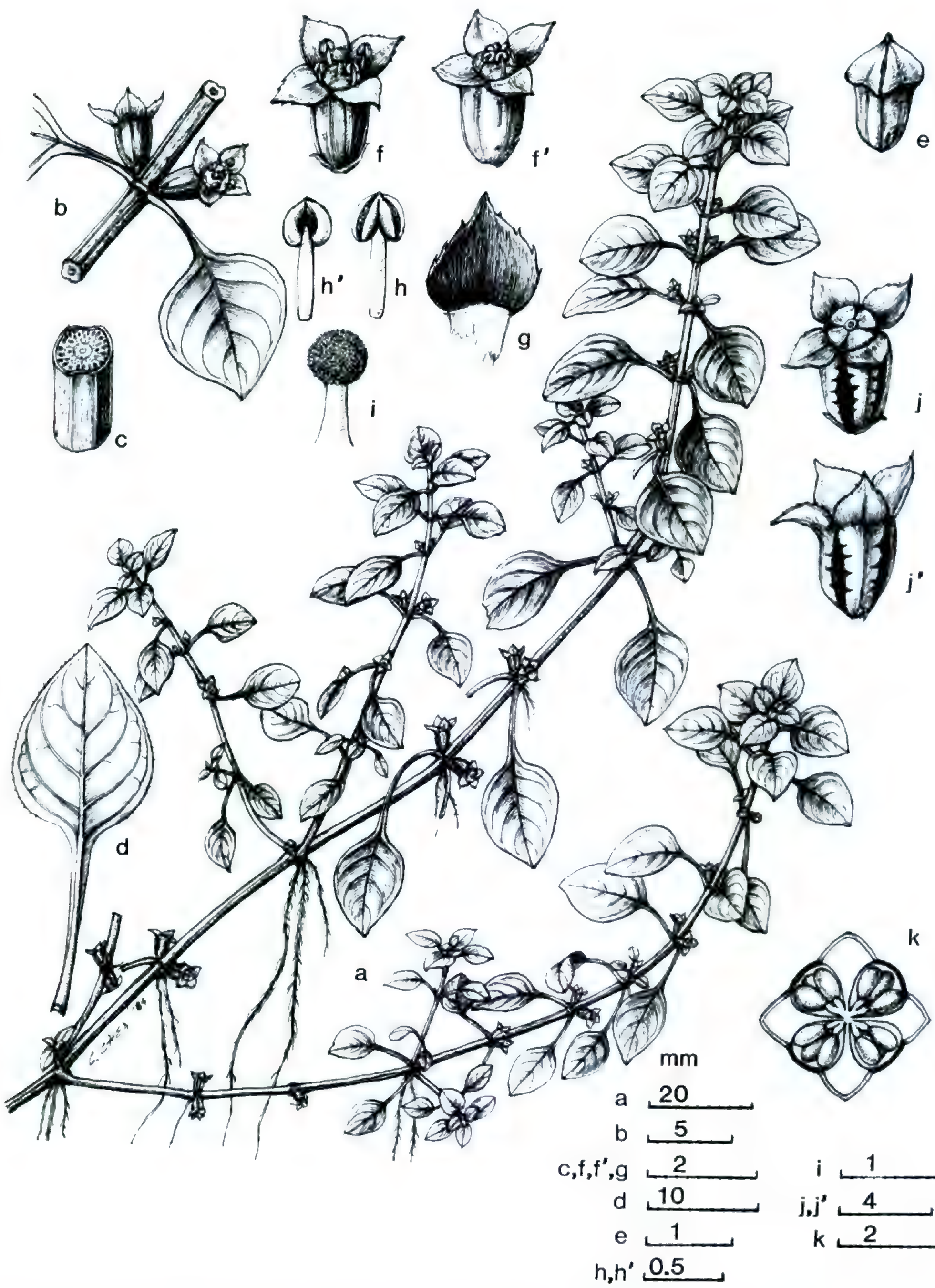

Figure 18. *Ludwigia palustris*; South Carolina, Berkeley Co., *Peng 4401* (MO). —a. Habit. —b. Portion of branch. —c. Portion of a stem. —d. Leaf. —e. Flower bud. —f, f'. Flower, early and late anthesis. —g. Sepal. —h, h'. Stamen, adaxial and abaxial view. —i. Stigma and style, with stigma covered with pollen. —j, j'. Fruit. —k. Fruit, cross section.

to Florida and west to eastern Minnesota, central Nebraska, and central Texas. This species also occurs along the Pacific coast from Vancouver Island, British Columbia, Canada, to southern California, with scattered occurrences in extreme southern Arizona and west Texas (Fig. 19). In Mexico, *L. palustris* occurs from Chihuahua, Nuevo León, Tamaulipas, and San Luis Potosí south to Michoacán, Veracruz, and Chiapas. *Ludwigia palustris* also extends through Guatemala and Costa Rica in Central America to Colombia and Venezuela in South America. In the Caribbean, this species has been found in Cuba, Jamaica, Haiti, Dominican Republic, and Puerto Rico (Fig. 20). In Eurasia, it occurs

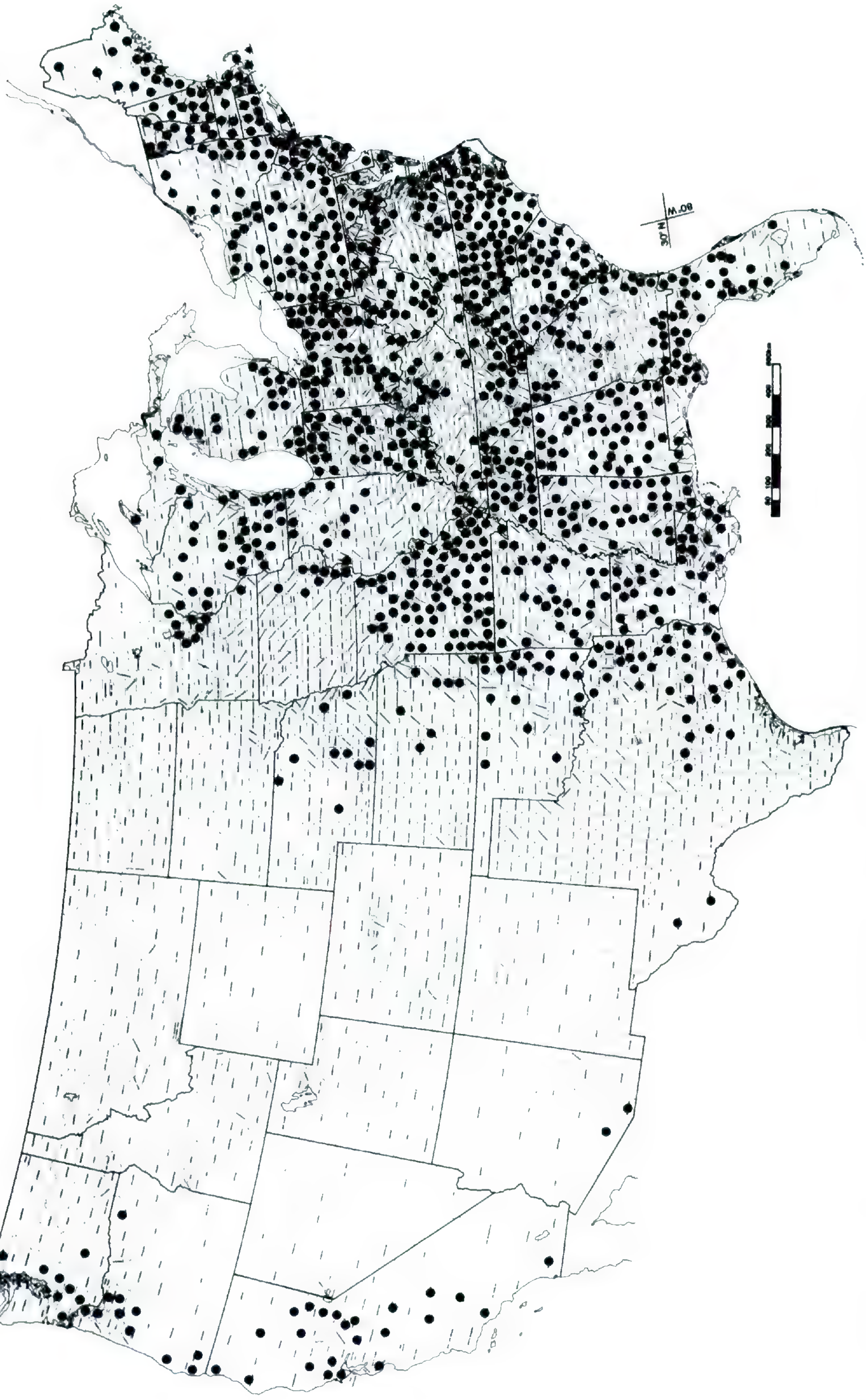

Figure 19. Distribution of *Ludwigia palustris* in the U.S.A.; see text for full listing of localities for *L. palustris* in Canada.

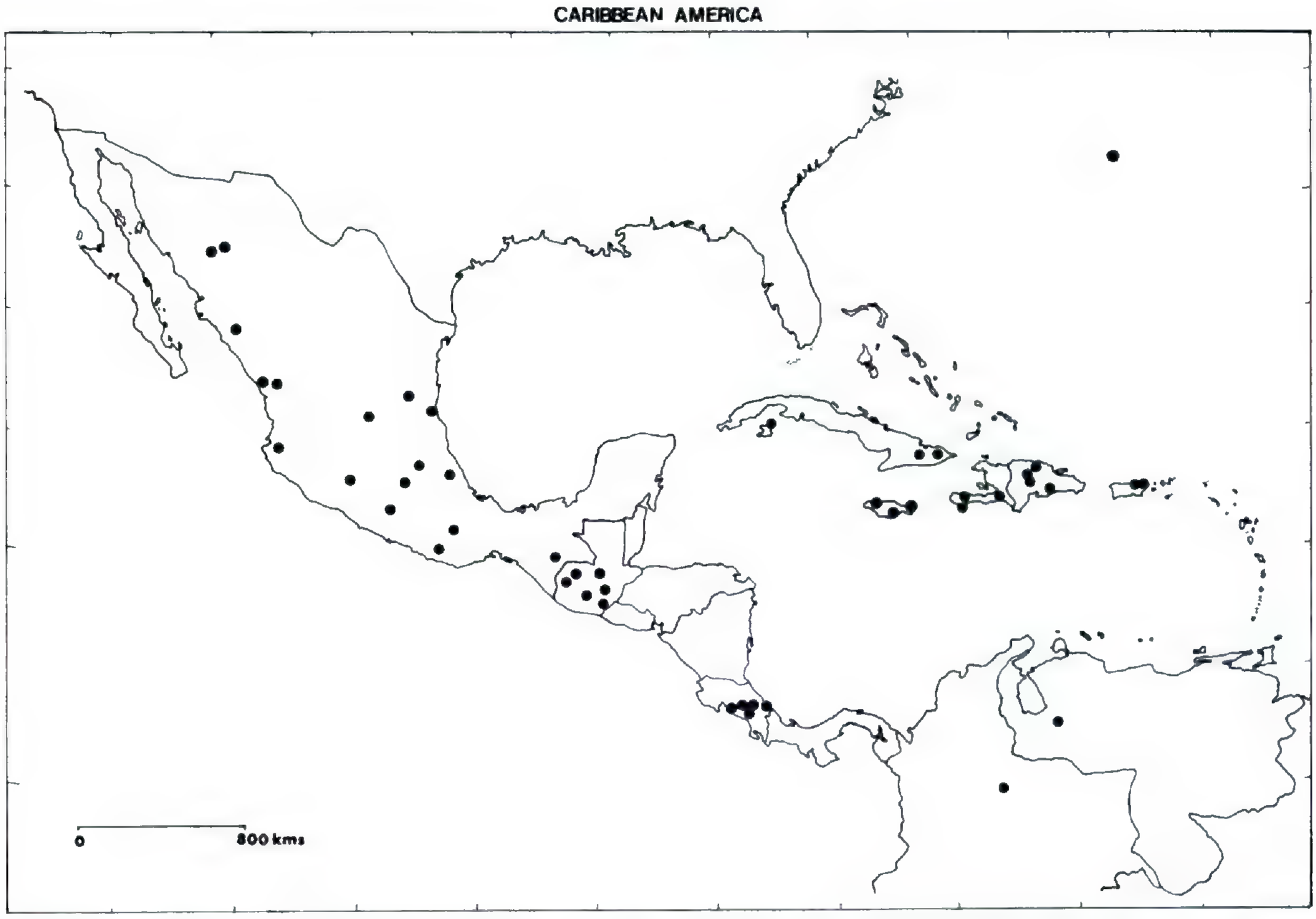

Figure 20. Distribution of *Ludwigia palustris* in Central America, South America, and the Caribbean region.

most commonly in western Europe (Raven, 1963a: fig. 18), from southern England, France, Portugal, and Spain eastward through the Netherlands, Belgium, Germany, Switzerland, Italy, Corsica, Austria, Poland, Czech Republic, Slovakia, Hungary, Croatia, Yugoslavia, Macedonia, Montenegro, Albania, Greece, Romania, and Bulgaria. It also occurs more sporadically in the Ukraine, the Caucasus region in Georgia, Anatolia in Turkey, and northern Iran. In Africa it occurs in coastal Morocco, Algeria, Tunisia, Socotra, southern Angola, Barotseland, Botswana, Namibia, Zimbabwe, and the Republic of South Africa (Raven, 1963a: fig. 18). It is introduced in the Hawaiian Islands, in New Zealand, and more recently in northeastern Victoria, Australia (Aston, 1967, 1973).

Habitat. Plants of *Ludwigia palustris* frequently form dense mats in roadside ditches, wet meadows, dried pond bottoms, along margins of ponds, swamps, rivers, edges of swamp forests, and alluvial sand bars along rivers. It grows mainly from sea level along coastal plains, but has been found up to 1000 m in California, 1220 m in Hawaiian Islands, 1300 m in southern Africa, and 2700 m in Mexico.

As noted under the sectional description, several authors subsequent to Linnaeus illegitimately based new names on *Isnardia palustris*, as follows: *Tiphogeton palustre* (L.) Ehrh., Beitr. 4: 146. 1789, nom. illegit.; *Dantia palustris* Petit ex Des Moul., Act. Soc. Linn. Bordeaux 20: 517. 1860, nom. illegit.; *Quadricosta palustris* (L.) Dulac, Fl. Hautes-Pyr. 329. 1867, nom. illegit.; and *Jussiaea isnardia* E. H. L. Krause, in Sturm., Fl. Deutschl. ed. 2. 9: 185. 1901, nom. illegit.

The holotype ("Lac Tonga, eastern Algeria," Apr. 1908, *Glück s.n.*—the only specimen that Glück mentioned collecting rather than just observing) and other authentic specimens of *Isnardia palustris* L. f. *submersa* Glück apparently were destroyed in Berlin in 1945, and no duplicates have been located, so we have designated the illustration in Glück's article as the lectotype. Eames (1933) made the combination *Ludwigia palustris* (L.) Elliott f. *submersa* (Glück) Eames, citing a submerged specimen from Connecticut as being the same taxon as described by Glück. Without providing any explanation, Fassett (Rhodora 41: 377. 1939) stated that Eames's specimen did not correspond to Glück's taxon, and illegitimately provided a new name (*L. palustris* var. *americana* (DC.) Fern. & Grisc. f. *elongata* Fassett) for Eames's taxon.

Ludwigia palustris is the most widely distributed species in section *Dantia* and probably in the genus as well. It is particularly widespread in temperate North America and Europe; the type is

thought to be from Europe. Candolle (1828) initially subdivided this species and proposed an infraspecific epithet for New World populations. Based primarily on capsule size and shape of leaves and sepals, Fernald and Griscom (1935) further subdivided the species and recognized four varieties that are frequently used, but several authors have challenged this classification (Duke, 1955; Traulau, 1959; Raven, 1963a; Munz, 1965). Traulau (1959) argued that differences in fruit color and size between the European variety *palustris* and the North American variety *americana* are overlapping and inconsistent. The other two varieties proposed by Fernald and Griscom (1935), *L. palustris* var. *nana* and variety *pacifica*, distributed respectively in the southeastern United States and on the Pacific coast, have smaller fruits and somewhat narrower leaves than variety *americana*. Duke (1955: 267) pointed out that in plants from drier sites in North Carolina, "the main axis of a plant may have large ovate leaves and thick fruits, while branches may have much shorter, narrower leaves and thinner fruits," suggesting that under drier conditions, the characters of variety *nana* may be environmentally produced. Duke found the same tendency for smaller fruits and narrow leaves in plants more distantly removed from a body of water. Similarly in England, Salisbury (1972: 34–35) found that "completely terrestrial plants [of *L. palustris*] are much smaller than the partially submerged plants growing in shallow water."

Raven (1963a) observed that much the same is true of *Ludwigia palustris* var. *pacifica*, which consists largely of plants that grow on drying lake beds and similar places in the western U.S., and are reduced in size of all parts, including fruits and leaves, sometimes being as small as 1.5 cm tall. Grown in moist common garden conditions, such plants are indistinguishable from other strains of the species. It is therefore our opinion that the evidence for the recognition of infraspecific taxa in *Ludwigia palustris* is insufficient.

Traulau (1959) considered that *Ludwigia palustris* is not native to the Old World. Raven (1963a) provided evidence that it was present in several widely separated areas in Europe as early as 1666, so it is quite unlikely to have been introduced there by any recent human activities. Furthermore, Raven pointed out that the place where it was found in England by 1666 (near Petersfield, Hampshire) is the same area of the country to which it is confined at present, some three centuries later. This sort of distribution pattern is not what one would expect of a recently introduced plant. Therefore, we suggest that *Ludwigia palustris* may be native to Europe as well as North America, or at least dispersed to Europe (e.g., via wading birds) prior to the European voyages of discovery. Moreover, the presence in eastern Asia of *L. ovalis* (monotypic sect. *Miquelia*), a haplostemonous species apparently closely related to section *Dantia* (Raven, 1963a), suggests that the north temperate lineage to which both sections *Dantia* and *Miquelia* belong may have had a fairly extensive history connected with the evolution of the Arcto-Tertiary Geoflora (Raven, 1963a).

Ludwigia palustris is the only diploid species in section *Dantia*. Diagnostic features of *L. palustris* include very broadly to narrowly elliptic leaves, small, apetalous, sessile flowers, and relatively thin-walled capsules with four longitudinal light green stripes. The green stripes are located in the placental radii and mark the thinnest area of the exocarp, which alternate with thicker exocarp that is tan in the septal radii (Salisbury, 1972; Eyde, 1978: fig. 10).

The only other species with which *Ludwigia palustris* may sometimes be confused, and then only when sterile specimens are concerned, is the hexaploid *L. repens*. Based on morphological and cytogenetic analysis, we consider *L. palustris* to be one of the putative parental species of *L. repens*.

As the most widespread species in section *Dantia*, *Ludwigia palustris* completely overlaps in distribution range with all other species. Natural hybrids are found between *L. palustris* and all taxa except *L. arcuata*, which has the largest flowers in the section. In experimental crosses we found that *L. arcuata* sets no seed when pollinated with *L. palustris* pollen. This may be due to the inability of small pollen of *L. palustris* (21 × 33 μm vs. 42 × 69 μm in *L. arcuata*—cf. Praglowski et al., 1983) to grow through the style of *L. arcuata*, which is six to seven times longer than that of *L. palustris* (Table 2). Reciprocal crosses were successful, but resulted in highly infertile offspring.

Although most plants of section *Dantia* have opposite leaves, some populations of *Ludwigia palustris* outside continental North America exhibit some alternate or subalternate leaves on predominantly opposite-leaved plants. These include plants from the U.S. (Hawaii: *Degener et al. 20204*); Dominican Republic (*Raunkiaer 896*); Haiti (*Holdridge 1990*); Namibia (*Merxmüller & Giess 30039*); and New Zealand (*Mason & Moar 80*). These collections may represent natural hybrids between opposite-leaved *Ludwigia palustris* and some related species of alternate-leaved *Ludwigia*, possibly of section *Microcarpium* or the monotypic section *Miquelia*. Such hybrids, however, would be highly sterile (Peng,

1988, unpublished), whereas the cited collections appear to be fully fertile with good seed set. Furthermore, other than phyllotaxy, these collections do not exhibit intermediate or aberrant characters. These unusual plants of *L. palustris*, many of which occur on oceanic islands, apparently arose spontaneously and may have persisted under altered conditions of selection.

Ludwigia palustris is perennial in cultivation and appears to be perennial throughout most of its native range. Salisbury (1972) noted, however, that populations from England may behave as annuals under conditions where the winter is severe. Similarly, some specimens from the northeastern United States (Maine, *Fassett 13487*, MO; New Hampshire, *Churchill s.n.*, MSU; Vermont, *Seymour & Countryman 22163*, MO) are laden with small fruits even though the whole plants are only 1–5 cm tall. Apparently such plants start to flower at a very early stage of development, which is a strategy associated with annual r-selected species.

Because they have not been mapped, all specimens examined of *Ludwigia palustris* from Canada that represent distinct localities are cited below.

Representative specimens examined. NORTH AMERICA. CANADA. **British Columbia:** Vancouver Island, Somenos Lake N of Duncan, *Calder & MacKay 31981* (DOA); Sproat Lake, 1887, *Macoun s.n.* (C, NA); Quamichan Lake, 1964, *Melburn s.n.* (DUKE). **New Brunswick:** Sunbury, St. John River, Burton, *Fassett 2286* (GH); St. John River, ca. 30 mi. N of St. John, *Scoggen 13070* (W); Fredericton, 1880, *Fowler s.n.* (NY); Sussex, ca. 45 mi. SW of Moncton, *Scoggen 13047* (W). **Nova Scotia:** Annapolis, Middleton, *Fernald & Pease 21987* (GH); Cape Breton, Sydney, 1902, *Fernald s.n.* (GH); Pottles Lake, North Sydney, *Bissell & Linden 21989* (GH); Cape Breton Island, Louisburg, *Macoun 19128* (GH); Colchester, Brookfield, *Dore & Roland 45997* (M); Cumberland, Shinimikas River, Northport, *Fassett 2287* (GH); Hants, Five Mile River, *Pease & Long 21986* (GH); Salmon River, Truro, *Bissell et al. 21985* (GH); Lunenburg, Lahave River above Bridgewater, *Fernald & Long 24201* (GH); Pictou, Charcoal, *St. John 1434* (CAS, CM, F, GH, NA, NY); Pictou, West River, *Robinson 490* (NY); Richmond, Point Michaud, *Duncan & Duncan 30085* (FLAS); Shelburne, East Jordan, *Fernald & Long 24199* (GH); Yarmouth, Ogden Lake, *Fernald & Long 24200* (C, GH); Salmon (Greenville) Lake, *Fernald & Long 21988* (GH); St. John Lake, Springhaven, *Fernald & Long 21990* (GH, S). **Ontario:** Stokes Bay, *Krotkov 9251* (TENN); Bruce, Colpoys Bay, *Fassett 19324* (NA); Elgin, 4 mi. S of St. Thomas, *James 1793* (F, W); Essex, 1 mi. SW of Windsor, *Rogers 9686* (MSC); Hastings, *Macoun 68* (GH); Norfolk, Charlotteville Turnpike, *Soper 2623* (GH); French River Harbor, *Grassel 2088* (MICH); Waterloo, 1 mi. S of Kitchener, *Montgomery 680* (GH); Casselman, 1891, *Scott s.n.* (C); Lake Muskoka, 1902, *Patterson s.n.* (CM); Ottawa, 1894, *Macoun s.n.* (MO); Plevna, 1902, *Fowler s.n.* (GH); Kingston, Battersea, 1898, *Fowler s.n.* (F); Wingham, 1891, *Morton s.n.* (NY). **Quebec:** Cté. Brome, Glen Sutton, *Marie-Victorin et al. 56227* (GH); Cté. Chambly, Saint Hubert, *Marie-Victorin et al. 28707* (GH, S); Cté. d'Huntingdon, Hemmingford, *Marie-Victorin et al. 56272* (F, MO, NY); Cté. Mégantic, Slaterpond, *Hende et al. 63-1242* (GH, MEXU); Cté. Richelieu, Sainte Anne de Sorel, *Marie-Victorin et al. 2276* (M, NY, SMU, W); Sainte-Victoire, *Marie-Victorin et al. 2222* (MO); Cté. St. Jean, Napierville, *Raymond & Cinq-Mars 1717* (S); Ottawa, Harrington Lake, *Dole & Gillett 16357* (U); Rock Forest, Magog River, *Pease 28492* (GH); Cté. Terrebonne, Fillions, 1951, *Louis-Marie & Lamarre s.n.* (S); Notre-Dame de Ham, canton d'Ham Nord, *Hamel & Brisson 15398* (CM); Cté. Wolfe, Lac Miroir, *Hamel & Brisson 18470* (VDB); Longueuil, *Marie-Victorin 239* (NA) ; South Bolton, George Pond, 1934, *Dore s.n.* (NY). MEXICO. **Chiapas:** Ch'encultik, *Breedlove & Smith 32091* (DS). **Chihuahua:** lake near Chuhuichupa, *Le Sueur 1256* (F, GH). **Guerrero:** Coyuca-Animas, Balsas, *Hinton et al. 5858* (GH, MEXU, NA, NY, P). **Hidalgo:** Zacualtipan, *Moore 5375* (MEXU). **Jalisco:** 8 km NE of Talpa de Allende, *Anderson 12804* (MICH). **México:** Laguna de Zempoala, 2750 m, *de Veg. Acuatica 150* (MEXU). **Michoacán:** 5 km N of Ario de Rosales, *Koeppen & Iltis s.n.* (ENCB). **Oaxaca:** Nanchititla, Temascaltepec, *Hinton et al. 7606* (US). **San Luis Potosí:** *Schaffner 531* (BM, C, CAS, F, M, MSC, NA, NY, S, UPS). **Sinaloa:** Mazatlan, *Brandegee s.n.* (UC). **Sonora:** Laguna Galara, *Liebmann 3849* (US). **Tamaulipas:** Gómez Farías, *Martin & Saravia 1228* (ENCB). **Veracruz:** Azalan, La Esmeralda, *Ventura 8150* (CAS, CTES, ENCB, LL, VDB). U.S.A. **Alabama:** Barbour Co., Lake Eufaula, ca. 5 mi. S of Eufaula, *Kral 33210* (ENCB, MO, SMU, TENN, VDB). **Arizona:** Santa Cruz Co., Nogales, *Crutchfield 3366* (LL). **Arkansas:** Monroe Co., Holly Grove, *Demaree 37431* (GA, GH, NCU, NO, SMU, VDB). **California:** Butte Co., 8 mi. N of Oroville, *Heller 11683* (CAS, DS, F, GH, MO, NY, ND-G, NY). **Connecticut:** New London Co., Old Lyme, *Eames 11579* (GH). **Delaware:** Sussex Co., 2 mi. N of Georgetown, *Fogg Jr. 4481* (GH, TENN). **District of Columbia:** Washington, *Holm s.n.* (C, CAS, NY). **Florida:** Leon Co., 2 mi. E of Tallahassee, *Godfrey 55595* (FLAS, GA, GH, LL, NY, SMU, TENN, UNA). **Georgia:** Whitfield Co., N of Dalton, *Wilson 107* (F, GH, MO, NA, NY). **Hawaii:** Hawai'i, along Saddle Rd. 23.5 mi. from Hilo, *Degener et al. 20204* (BISH, GH, K, MO, NY, UC, US). **Illinois:** St. Clair Co., SW of Marissa, *Neill 15430* (MO, NCU). **Indiana:** Orange Co., Chatham Pond, 4.5 mi. SW of Peipsic, *Friesner 20827* (LIL, MO, S, TEX). **Iowa:** Jones Co., Hale Twp., *Cooperrider 2747* (NCU). **Kansas:** Riley Co., *Norton 156* (JE, MO, NA, NY). **Kentucky:** Harlan Co., near Harlan Court House, *Kearney Jr. 31* (CHI, F, GA, MO, MSU, NA, NCU, NY, S). **Louisiana:** Franklin Parish, Civitan Park, Winnsboro, *Thieret 30049* (DS, DUKE, FLAS, GA, SMU, VDB). **Maine:** Piscataquis Co., Foxcroft, *Fernald 440* (GH, MO, MSC, NA). **Maryland:** Harford Co., 0.5 mi. SSW of Havre de Grace, *Shull 149* (MO, NA, NY). **Massachusetts:** Barnstable Co., Wellfleet, *Fernald & Fogg 570* (C, CAS, DUKE, DS, F, GA, GH, MO, MSC, NA, NCU, NO, NY, SMU, TENN, TEX, UPS). **Michigan:** Washtenaw Co., U. Michigan Botanical Gardens, *Herman 9122* (GA, MO, NY). **Minnesota:** Mille Lacs Co., Milaca, *Sheldon s.n.* (GH, NA, NY, S). **Mississippi:** Madison Co., Wildlife Refuge, SE of Canton, Ross Barnett Res., *Chapman et al. 18037* (GA, MISS, NCU, VDB). **Missouri:** Caldwell Co., Shoal Creek, 7.5 mi. NW of Braymer, *Steyermark 6045* (F, MO). **Nebraska:** Hall Co., Grand Island, *Kiener 15109* (F, W). **New Hampshire:** Cheshire Co., Rte. 123 near Alstead line, *Boufford 7761* (MO). **New Jersey:** Camden Co., Delair, *Pennell*

12003 (CM, NY). **New York:** Dutchess Co., Stony Creek Red Hock, *Elwert & Svenson 6446* (CAS, F, GH, MO, NY, US, WISC). **North Carolina:** Carteret Co., E of Newport, *Godfrey 49846* (FLAS, GH, LIL, MO, VA, NCSC, NY, SMU). **Ohio:** Huron Co., W of New Haven, *Jones 67-10-22-1339* (FSU, TENN). **Oklahoma:** Sequoyah Co., 1 mi. NE of Gore, *Wallis 7734* (GA, GH, NCU, NO, SMU, TEX). **Oregon:** Multnomah Co., University Park, *Sheldon s.n.* (DS, F, GH, MO, NA, NY). **Pennsylvania:** Bucks Co., Swamp Creek, Finland, *Benner s.n.* (CM, GH). **Rhode Island:** Washington Co., Hopkinton, *Fernald et al. s.n.* (GH). **South Carolina:** Berkeley Co., Santee River near Jamestown, *Godfrey & Tryon Jr. 125* (CAS, DUKE, F, GH, MO, NA, NY, TENN). **Tennessee:** Hickman Co., Centerville, *Kral 31546* (SMU, TENN, VDB). **Texas:** Gonzales Co., Ottine, *Tharp s.n.* (MO, NY, SMU, TEX). **Vermont:** Franklin Co., bridge of Lamoille River, *Fairfax et al. 24403* (MO, SMU). **Virginia:** Accomack Co., 3.5 mi. N of Accomack, *Fernald et al. 5390* (GH, MO, NY). **Washington:** Thurston Co., 4 mi. E of Olympia, *Hitchcock 24113* (NY). **West Virginia:** Wirt Co., Palestine, *Bartholomew W1941-903* (FLAS, GA, GH, NY, SMU, TAES, TENN, UNA). **Wisconsin:** Jefferson Co., Farmers Isl., Lake Mills, *Botany 162 class s.n.* (DUKE, F, MO, NY, UNA).

CENTRAL AMERICA. COSTA RICA. **Alajuela:** Capulin, *Standley 40098* (NA). **Cartago:** Tapanti, *Alameda et al. 3024* (CAS, MO). **Limón:** Puerto Limón, *Kuntze s.n.* (NY). **San José:** finca La Cabana, *Weston et al. 4860* (MO, UC). GUATEMALA. **Alta Verapaz:** Cobán, *Türckheim 784* (E, NA, US). **Baja Verapaz:** Puralhá, *Türckheim 1720* (E, G, GH, US, W). **Huehuetenango:** Laguna de Ocubilá, *Standley 82693* (F). **Jalapa:** Potrero Carrillo, *Steyermark 33108* (F). **Jutiapa:** near Jutiapa, *Standley 60526* (F). **Quiché:** Río de las Violetas, N of Nebaj, *Proctor 25205* (LL). **Sacatepequez:** Antigua, 1841, *s.c. s.n.* (C).

CARIBBEAN. BERMUDA. Pembroke Marsh, *Brown et al. 2123* (GH, NA, NY). CUBA. **Guantanamo:** Monte Verde dictam, *Wright 157* (GH, W). **Isla de la Juventud:** Isle of Pines, Nueva Gerona, *Killip 45595* (US). **Santiago de Cuba:** La Perla, *Shafer 8725* (U). DOMINICAN REPUBLIC. **Azua:** Monte Culo de Mars, *Fuertes 1914* (GH, NY). **Distrito Nacional:** Santo Domingo, La Caleta, *Ekman 10937* (G, GH, NA, NY, S, US). **La Vega:** Propo Constanza, *Türckheim 3290* (BM, E, G, GH, L, M, MO, NA, NY, S, U, W). **Puerto Plata:** Gurabito de Yoroa, *Liogier 16191* (NA, NY). **Santiago:** Santiago, *Raunkiaer 896* (C). HAITI. **Sud:** Massif de la Hotte, Pestel at Delcour, *Ekman 9013* (LL, NA, S, US). **Ouest:** near Savane du Louis, *Holdridge 1990* (F, MO). JAMAICA. **Manchester:** St. Thomas, Morant River at Morant Bay, *Proctor 31575* (F). **Trelawny:** lake at Dromilly, *Proctor 15700* (GH). PUERTO RICO. **Humacao:** La Sardinera, *Britton & Britton 9522* (NA, NY, US). **San Juan:** vicinity of Dorado, *Britton et al. 6702* (F, NA, NY, US).

SOUTH AMERICA. COLOMBIA. Boca Sogamoso, Río Magdalena, *Pennell 3848* (GH, NA, NY). VENEZUELA. **Mérida:** above La Carbonera, *Steyermark 56008* (F, NA, NY, US).

EUROPE. AUSTRIA. Lustbühel prope urbem Graz, *Fritsch s.n.* (ND, W); Prov. Klagenfurt, Carinthia, *Jabarnegg s.n.* (JE); Wiesberges bei Leibruntz, *Schellauf 346* (B); Waltendorf bei Graz, *Eggler 346* (B). BELGIUM. Aerschot, *Devos 76* (JE); Brabant prov. Beggneudgh, *Dieudonne s.n.* (S). CZECH REPUBLIC. Distr. Bereg, *Margittai 349* (GH, MO, NA, S, W). FRANCE. Solenzara, *Aellen 2458* (F, MO, NA); Bord de rivière Saint-Nicolas, Belfort, *Parisot s.n.* (JE, S, W, WAG); Montbeliard, *Contejean s.n.* (JE, S, WAG); Le Cannet des Maures, *Berger 4326* (AAU, M); Villas-les-Dombes, *Thiébaut 3021* (S); Somme, Abbeville, *Nicy s.n.* (W); Bretagne, Rosporden, *Hafshom s.n.* (S); Judre-et-Soire, *Blanchet s.n.* (C, DS, F, MO); Rambervilles (Nosger), *Boulay s.n.* (DS); La Vieille Fontaine, *Souche 2846* (DS); lac d'Aureilham, *Butler 963* (NY); Champvans près Dole jura, *Blanche s.n.* (NA, DS); Puy-de-Dôme, Lezoux, *Chassagne 3021* (B); Rocologne, *Godet s.n.* (GH); Biarritz, *Lang s.n.* (C); Loire Cuzieu, *Outhenting s.n.* (F). GERMANY. Büchen, *Becker 801* (JE, WAG); Pfalz Knittelsheimer Gänseweide, *Hoock s.n.* (GH, M); Dulmen, *Tali s.n.* (M); Frankfurt, *Dürer s.n.* (JE); Ofenbach, *Haussknecht s.n.* (JE); Gangelt, Schanze, Auchen, *Brigener s.n.* (JE); Hanover, *Ehrhart 13* (M, W); Hemsendorf, *Casper & Ksausch s.n.* (JE); Gangelt, Linz, Aachen, *Monheim s.n.* (W); Dulman, *Hanby 221E* (RB); Moosburg, *Drobny s.n.* (W); Rosenthal, *Korb s.n.* (W); Eppendorfen, *Haimburg s.n.* (W); Rheinpfalz, *Kock s.n.* (M); Westfalen, Dulman, Lüskenbruch, *Reiss s.n.* (S); Korb bei Kehl, *Schimpar s.n.* (F); Hanover, *Meier s.n.* (F); Lachtehausen bei Celle, *Nöldeke 394* (NA); Rufo, Hanau, *Sohliskum s.n.* (B); Knittelsheim of Landau, *Hooch s.n.* (C); Carlsruhe, *Brauns s.n.* (NY); Sachsen, Schünewalke, *Matthies s.n.* (B); Jecklanburg, *Hederman s.n.* (AAU); Hommersum, *Herrenkohl s.n.* (B); Hochdorf, *Whlatterer s.n.* (B); Lürkan, *Schultz s.n.* (B); Muhlburg, *Kneuker & Karsrahe s.n.* (B). GREAT BRITAIN. Sussex Co., *Babington s.n.* (C); Hampshire Co., Hatchet Pond near Beaulieu, *Raven 16321* (MO). GREECE. Makedonya, *Bornmüller & Burgelf 1595* (JE). HUNGARY. Comit. Vas, Kam, *Gayer s.n.* (C, F, M, S, W); Comit. Akad. Bokoszeg, *Simonkai 2458* (B, C, GH, M, MO, S, W). ITALY. Vernoae, Cólà, *Rigo s.n.* (B, W); Pisa, *Sair s.n.* (F, JE); Turin/Piedmont, *Fortana s.n.* (M); Colico, *Vidal s.n.* (JE); Longobardie, Peon. Mantrige, *Rigo s.n.* (JE); Montua Lombardizy, *Pittoni s.n.* (W); Risoje di Gravellone (Pavia), *Cinepa s.n.* (S); Monfalcóne, *Vobl s.n.* (C); San Pancrazio, *Perrier de la Bâthie s.n.* (GH, MO); Tuscany, *Pisano s.n.* (F); Pisana, *Savi s.n.* (GH); Silva Pisana, *Ball s.n.* (CHI); Candia Canavese, Rorino, *Crosetti s.n.* (AAU). (Former Yugoslav Republic of) MACEDONIA. Dojran, *Seinfer 1595* (M). NETHERLANDS. Overyssel, Denekamp, *Bremer s.n.* (WAG); Broekwolen, *Suringar s.n.* (WAG). PORTUGAL. Terra de Monchique, Algarre, *Bourgeau s.n.* (WAG); Lusitania-Beira-Litoral, Mira, *Rainha 1465* (S); Lusitaniae, Beira Baisca, Covitha, *Liha 1084* (S); Beira-Litoral, Coimbra, *Lilva 1667* (S); Lusitani, Ribatejo, *Rainba 3612* (NA, S). ROMANIA. Oltenia, distr. Craiova, *Malos et al. s.n.* (B, NY). SPAIN. Catalogne, Marécages, *Augustin 1110* (W). SWITZERLAND. Genève, St. Tulien, *Heldreich s.n.* (M); Baden-Wurttemberg, Hochdorf, *Dörr s.n.* (M), Opfingen, *Reitzenstein s.n.* (M); Lachsen, *Schweinitz s.n.* (M); Aargau, Rohrdorfer Moor, *Scheitz s.n.* (JE); Cordola, Tessin, *Muret s.n.* (JE); Lugano, *Boissier s.n.* (MO); Kt. Tessin, Riazzino, *Berger s.n.* (B, S); Interlaken, *Hofman Barg s.n.* (NCU).

ASIA. IRAN. Prope Rascht, *Bornmüller 7011* (B). TURKEY. Persia, Rescht, *Lipsky s.n.* (JE).

AFRICA. BOTSWANA. 23 km SE of Maun, *Biegel & Russell 3731A* (M, MO, WAG); Okavango swamps, Kahajo, *Smith 1141* (B, MO). NAMIBIA. Otjiwarongo, *Merxmüller & Giess 30039* (M, WAG). REPUBLIC OF SOUTH AFRICA. **Letaba:** Duiwelskloof, Merensky Dam, *Scheepers 1181* (B, M, S, W). **Natal:** Polela, *Acocks 22131* (S); Champaign Castle, Crakeusberge, *Meebold 13175* (M); Klip River distr., NE of Van Reenen, *Hilliard & Burit*

9470 (MO). **Swellendam:** Kochmanskloof, *Eiklon 1763* (W). **Transvaal:** Pretoria, *Meebold 16738* (M). ZIMBABWE. Harare ("Salisbury"), *Wild 14919* (MO); Gwebi, 1960, *Rutherford-Smith s.n.* (DS), Hunyani River at jct. of Gwebi River, *Gibbs Russel 2493* (GA, MO); 12 km SW of Mazoe, *Biegel & Pope s.n.* (B, MO); Bechuanaland, Totem, *Wild & Drummond 7150* (DS).

AUSTRALASIA. NEW ZEALAND. North Island: Kaihu River, *Mason & Moar 80* (CHR, MO); Mermere, Waikato Basin, *Robaroto 1007* (AKU, MO); Braemar Lagoon, 6.5 mi. S of Matata, *Mason 9648* (CHR, MO); Gollan's Valley, Wellington, *Mason s.n.* (CHR, MO); Kaitoke, Great Barrier Island, *Mason 441* (CHR, MO); Piako Co., 10 km SE of Le Aroha, *Bartlett s.n.* (AK, MO); Reglan Co., Lake Whangape, *Orchard 4877* (A, AK, MO); Otekairangi, North Auckland, *Mason & Moar 408* (CHR, MO); Rotorua Co., Lake Rerewhakaaitu, *Mason 9899* (CHR, MO); Kerikeri Inlet Rd., *Mason & Moar 356* (CHR, MO); Golden Springs, Rotorua-Taupo Hwy., *Mason 9892* (CHR, MO).

2. Ludwigia spathulata Torr. & A. Gray, Fl. N. Amer. 1: 526. 1840. *Isnardia spathulata* (Torr. & A. Gray) Kuntze, Rev. Gen. Pl. 1: 251. 1891. TYPE: U.S.A. "Middle Florida," s.d., *A. W. Chapman s.n.* (holotype, NY!; isotypes, F [2]!, GH [2]!, GOET!, MO!, NY!, P!, UPS!, US!). Figures 1–3, 21.

Perennial herbs with prostrate stems, rooting at the nodes, 10–40 cm long, well-branched, ascending at the tips, plants densely strigillose throughout, the hairs 0.25–0.7 mm long. Leaves elliptic-spatulate or narrowly so, the blades 9–17 × 3.3–9 mm, strigillose, apex acute, margin entire, base attenuate into a very narrowly winged petiole 3–9 mm long; stipules minute, reddish brown, narrowly ovate, 0.1–0.2 × 0.05–0.1 mm; bracteoles minute and often obscured by hairs, narrowly oblong or oblanceolate, 0.2–0.8 × 0.05–0.2 mm, flanking capsule base or on short pedicel. Flowers axillary and usually paired; sepals green, broadly ovate to deltate, 1–1.7 × 1.1–1.7 mm, ascending, densely strigillose without, glabrous within, apex acuminate, margin entire and densely strigillose; petals absent; anthers 0.2–0.35 × 0.3–0.5 mm; filaments translucent, 0.5–0.8 mm long; pollen shed singly; nectary disc yellowish green, raised 0.1–0.15 mm on ovary apex, appears flat upon drying, 0.7–0.85 mm across, 4-lobed, glabrous; style yellowish green, 0.25–0.5 mm long, glabrous; stigma pale yellow, 0.15–0.18 × 0.2–0.25 mm. Capsules light brown, oblong-obovoid, 2.5–4(–4.5) mm long, 1.5–2.5 mm thick, thin-walled, the loculicidal radii often appearing as alternating longitudinal green bands, sessile or on pedicels 0.1–0.5 mm long. Seeds dark reddish brown, ellipsoid, 0.55–0.7 × 0.4–0.45 mm, often visible on exocarp as small bumps, the surface cells transversely elongate. Self-compatible. Gametic chromosome number, $n = 16$.

Phenology. Flowering from May to September; fruiting from June to October.

Distribution (Fig. 22). *Ludwigia spathulata* occurs primarily in the Gulf Coastal Plain of the United States, in southern Alabama, the panhandle of Florida, and extreme southwestern Georgia. Several outlying populations have also been collected in the transitional areas between the Coastal Plain and the Piedmont in South Carolina and Georgia.

Habitat. Plants of *L. spathulata* are found in ditches, swales, shores of ponds or lakes, sink or swamp margins, sandy river bottoms, dried up pond bottoms, and disturbed low savannas.

Ludwigia spathulata is a rare species with the most restricted range within section *Dantia*. It is also the least variable species in the section. Its closest affinity is definitely with *L. palustris*, which is shown in this study to be one of its probable diploid progenitors. Biosystematic studies suggest that *L. spathulata* was derived from hybridization between *L. palustris* and a presumably extinct diploid species with a genome not found in any extant species of section *Dantia*. In both species, the modally autogamous flowers are small, apetalous, and subsessile, with pollen shed singly. The capsule exocarp is relatively thin, especially in the loculicidal radii, which, like those of *L. palustris*, often appear as alternating longitudinal green bands under which the seeds are somewhat visible as small bumps.

Ludwigia spathulata is readily distinguished from *L. palustris*, however, in being densely strigillose throughout and having dark reddish brown seeds. Leaf shape and size, which are highly variable in *Ludwigia palustris*, are rather uniform in *L. spathulata*, being elliptic-spatulate or narrowly so, ranging from 9–17 × 3.3–9 mm (vs. 5.5–45 × 2.5–23 mm in *L. palustris*). The leaves of *L. spathulata* also tend to be paler green than those of other species in section *Dantia* and are rarely flushed with red.

All populations of *Ludwigia spathulata* occur within the range of *L. palustris*. Except for *L. brevipes*, all other species in section *Dantia* slightly overlap with *L. spathulata* in the borders of their ranges. Natural hybrids are known only between *L. spathulata* and *L. palustris* (see *Hybrids*). The triploid hybrids resemble *L. spathulata*, but the strigillose hairs are shorter, the pollen is almost all sterile, and the ovaries turn yellow or pink after anthesis, and then abort. They are comparable to experimental hybrids of the same combination in morphology (Fig. 7). In the experimental greenhouse, we have crossed *L. spathulata* successfully

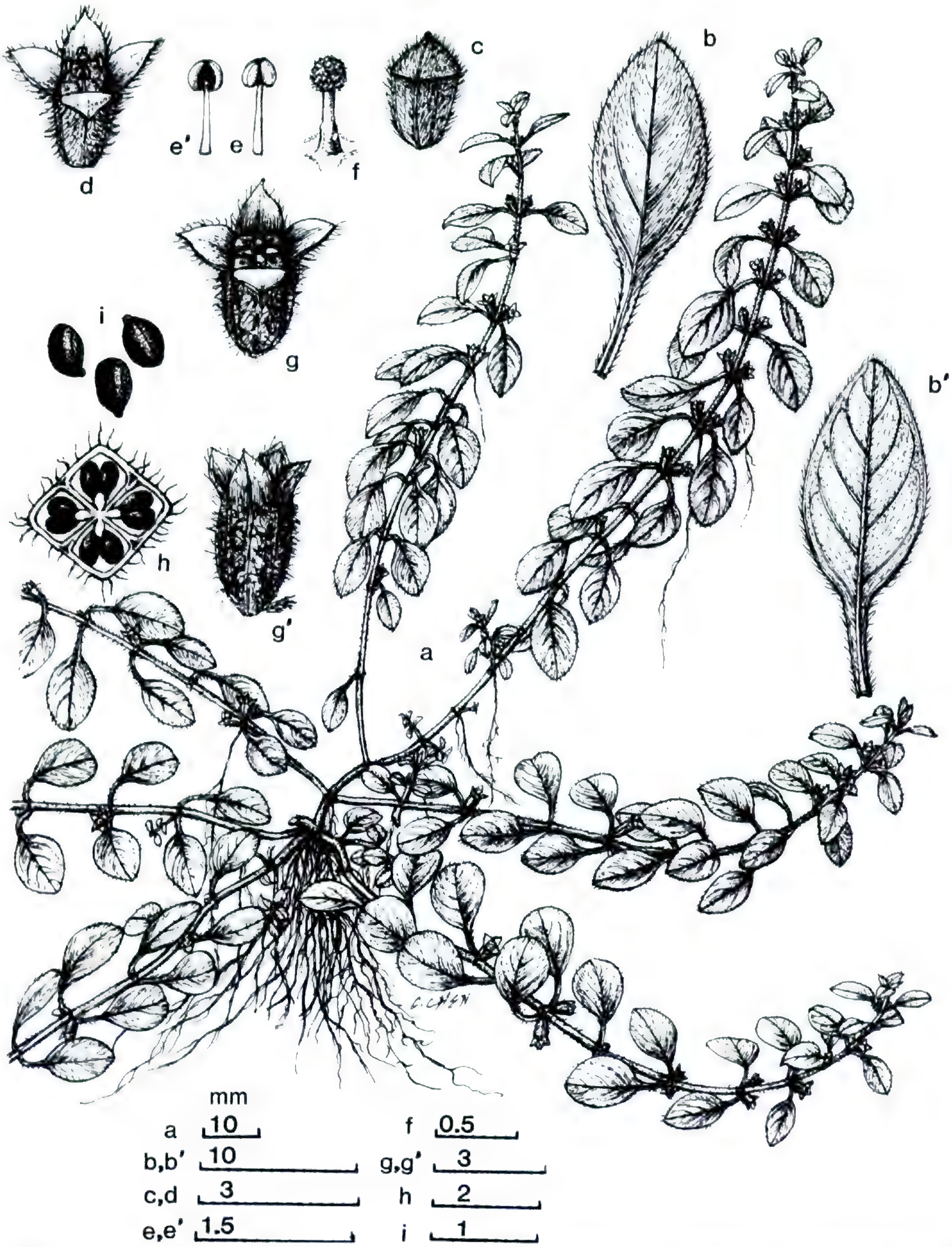

Figure 21. *Ludwigia spathulata*: Florida, Jackson Co., *Godfrey 77099* (MO). —a. Habit. —b, b'. Leaf, adaxial and abaxial surface. —c. Flower bud. —d. Flower. —e, e'. Stamens, adaxial and abaxial view. —f. Stigma and style, with stigma covered with pollen. —g, g'. Fruit. —h. Fruit, cross section. —i. Seeds.

with all other species to form vigorous but sterile F_1 hybrids.

Representative specimens examined. NORTH AMERICA. U.S.A. **Alabama:** Baldwin Co., S of Perdido, *Kral 38179* (VDB); Barbour Co., Lake Eufaula, *Kral 33226* (ENCB, G, M, MO, PH, SMU, TENN, US, USF, VDB); Covington Co., Lake Jackson at Florala, *Kral 36818* (ENCB, GA, GH, MO, NCU, PH, US, VDB); Escambia Co., Conecuh River, 6 mi. E of Boykin, *Kral 44839* (MO, NCU, NY, US, VDB); Geneva Co., 1 mi. SW of Hartford, *McDaniel 7646* (FSU, VDB); Houston Co., Indigo Pond,

Figure 22. Distribution of *Ludwigia spathulata* (left) and *L. brevipes* (right).

Kral 52352 (VDB). **Florida:** Gadsden Co., 0.1 mi. S of FL Hwy. 269 on FL Hwy. 270, *Boufford et al. 18564* (CM, MO, NCU); Leon Co., 2 mi. N of Woodville, *Godfrey & Houk 62880* (AAU, CAS, DUKE, FLAS, FSU, ISC, MICH, MO, NA, NCU, NY, S, SMU, SP, TEX, USF, VDB); Jackson Co., 2–3 mi. W of Butler, *Godfrey & Henderson 62937* (DUKE, FLAS, FSU, LAF, MO, MSC, NCU, NY, SMU, TEX, US, USF, VDB); Walton Co., De Funiak Springs, *Curtiss 6853* (GA, GH, MIN, MO, NY, S, US, WISC). **Georgia:** Decatur Co., 1.3 mi. SSW of Faceville, *Thorne & Davidson 17149* (CU, FSU, IA); Meriwether Co., Nat'l. Fish Hatchery, Warm Springs, *Jones 21204* (GA, NCU); Mitchell Co., 4 mi. SW of Camilla, *Duncan 6683* (G, GA, KY, LAF, MISS); Oglethorpe Co., Echols Mill, 9.3 mi. NE of Lexington, *Montgomery 946* (GA). **South Carolina:** Aiken Co., 0.6 mi. NW of jct. of Co. Rts. 55 & 273 at White Pond, *Leonard et al. 4992* (BOON, C, CM, CTES, ECUH, FLAS, FSU, MEXU, MISS, MO, NO, NY, S, SMU, TENN, TEX, U, UNA, USCH, VDB, WCUH); Saluda Co., W of Ridge Spring on Hwy. 23, *Massey & Massey 2998* (NCU).

3. **Ludwigia arcuata** Walter, Fl. Car. 89. 1788. *Isnardia arcuata* (Walter) Kuntze, Rev. Gen. Pl. 1: 251. 1891. *Ludwigiantha arcuata* (Walter) Small, Bull. Torrey Bot. Club 24: 178. 1897. TYPE: U.S.A. South Carolina, vicinity of Berkeley Co., 1768–1788, *T. Walter s.n.* (holotype, *Walter Herbarium 66* lower left-hand specimen, BM not seen; microfiche!). Figures 1–3, 23.

Ludwigia pedunculosa Michx., Fl. Bor.-Amer. 1: 88. 1803. *Isnardia pedunculosa* (Michx.) DC., Prodr. 3: 60. 1828. TYPE: U.S.A. "In paludosis submaritimis Carolinae inferioris" [South Carolina], 1794, *A. Michaux s.n.* (holotype, P!; photo of holotype, GH!, MO!; isotypes, P [2]!, PH!).

Perennial herbs with prostrate stems, rooting at the nodes, 5–70 mm long, subglabrous to sparingly strigillose, more densely so near the tips, the hairs 0.1–0.2 mm long, often well-branched and forming mats, erect or ascending at the tips. Emergent leaves narrowly elliptic or oblanceolate-elliptic to linear, 6–18 × 1.2–5 mm (submerged leaves usually narrowly linear, 19–40 × 0.9–2.4 mm), glabrous to sparingly strigillose on margins and abaxial midveins, the hairs ca. 0.05 mm long, apex acute, margin entire, base narrowly cuneate, sessile or with petioles up to 2 mm long; stipules minute, reddish green, narrowly ovate-deltate, 0.1–0.15 × 0.07–0.1 mm, succulent; bracteoles sublinear or very narrowly elliptic, 1.4–5 × 0.15–0.75 mm, mi-

Figure 23. *Ludwigia arcuata*: Florida, Hillsborough Co., *Peng et al. 4330* (MO). —a, a′. Habit. —b. Leaf. —c. Stem cross section. —d. Flower. —e. Sepal. —f. Petal. —g. Adaxial and abaxial view of stamen. —h. Flower, stamens and petals removed to show stigma, style, and disc. —i. Fruit. —j. Fruit, cross section. —k. Fruit, longitudinal section.

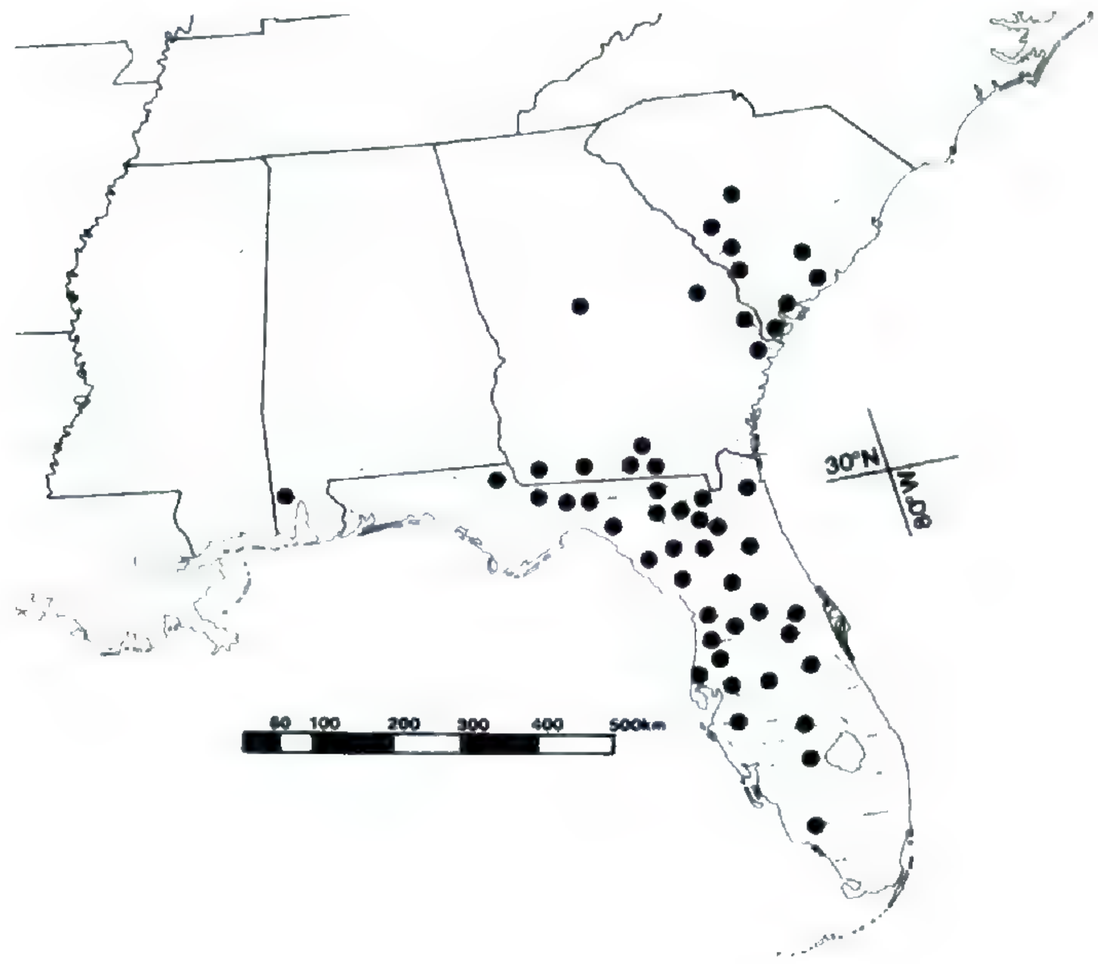

Figure 24. Distribution of *Ludwigia arcuata*.

nutely strigillose, flanking capsule base or attached 1.5–8 mm below capsule base on the pedicels. Flowers axillary and paired, relatively few; sepals green, narrowly triangular, 5.2–10 × 1.5–2.7 mm, with 3 parallel veins, often reflexed at anthesis, spreading to ascending in fruit, minutely strigillose on margins and abaxial surface, the hairs 0.05–0.15 mm long, apex very narrowly acute or elongate acuminate, margin entire; petals yellow, elliptic-obovate to spatulate-obovate, 7–11 × 4.5–8 mm, apex rounded, base attenuate; anthers lanceolate-oblong, 1.3–2 mm long; filaments yellow, 2.5–4.5 mm long, attached 0.35–0.45 mm above anther base; pollen shed in tight tetrads; nectary disc bright yellow, elevated 0.6–1 mm on ovary summit, 1.5–2.6 mm across, distinctly 4-lobed, the lobes dome shaped, minutely strigillose between disc lobes and sometimes on lobes as well, or glabrous; style yellow, 2.3–4(–4.8) mm long, glabrous; stigma yellow, capitate, 0.3–0.6 mm long, 0.6–1.8 mm thick. Capsules clavate, sometimes slightly curved, 5.5–10 mm long, 2.3–4 mm thick, usually minutely strigillose, the hairs 0.1–0.25 mm long, rarely glabrous, pedicels (12–)17–45 mm long, minutely strigillose. Seeds light to dark brown, elliptic-oblong, 0.55–0.65 × 0.3–0.35 mm, surface cells transversely elongate. Self-compatible. Gametic chromosome number, $n = 16$.

Phenology. Flowering from March to August; fruiting from May to October.

Distribution (Fig. 24). *Ludwigia arcuata* is endemic to the southeastern United States, occurring widely in the central and western parts of peninsular Florida and adjacent Georgia, extending into southern South Carolina and east-central Georgia. Disjunct populations have been collected in Bibb County in central Georgia and Mobile County, Alabama.

Habitat. Plants of *Ludwigia arcuata* grow in roadside ditches, edges of lakes or ponds, swampy prairies, springy places, and mucky or sandy beach strands.

Ludwigia arcuata is a distinctive species with small, narrow leaves and large, showy flowers that are elevated well above the dense mats of foliage by the elongate pedicels. It is the most consistently outcrossing species in section *Dantia*, judging by the showy petals, large anthers with abundant pollen shed as tight tetrads, well-elevated nectary disc that secretes copious nectar, and delay in arching of stamens toward the stigma to effect self-pollination at late anthesis. We observed abundant insect visitation on plants both in the field and under cultivation.

Drastically dissimilar to *Ludwigia spathulata* in morphology, *L. arcuata* is the only other tetraploid in section *Dantia*. Cytological analysis suggests that the two tetraploid species do not share any genome in common.

Ludwigia arcuata (BBCC) is sometimes confused with the hexaploid *L. brevipes* (AABBCC), but it has larger petals (7–11 mm vs. 4.5–5.2 mm long), longer pedicels ((12–)17–45 mm vs. (4.5–)6–15(–20) mm long), narrower leaves ((0.9–)1.2–5 mm vs. 2–7(–10.5) mm wide), and pollen shed in tight versus very loose tetrads. In fact, the two species share two diploid genomes, and the latter may have been derived following hybridization between the former and the diploid *L. palustris* (AA), which has much smaller, apetalous, sessile flowers that shed pollen singly. The ranges of *L. arcuata* and *L. brevipes* overlap only in South Carolina. Natural hybridiza-

tion between the two primarily outcrossing species is certainly possible, but such hybrids would be difficult to discern, given their morphological similarities. Artificial hybrids between them resemble *L. arcuata* (Fig. 13), have moderately fertile pollen (83%–90%; Table 4), and set at least some fertile seeds.

The range of *Ludwigia arcuata* overlaps those of all species of section *Dantia*. It hybridizes readily with the other hexaploid species, *L. repens*, in peninsular Florida (Fig. 4), where mixed populations of the two are common. Such hybrids show morphological intermediacy between the parents (Fig. 14), have about 54%–60% stainable pollen (Table 4), and set at least some fertile fruits.

Representative specimens cited. NORTH AMERICA. U.S.A. **Alabama:** Mobile Co., Dauphin Island, *Deramus D119* (MO, UNA). **Florida:** Alachua Co., 3 mi. SE of Hawthorne, *Godfrey & Reinert 61100* (MSC, NA, SMU, US, VDB); Baker Co., McClenny, *Lighthipe 514* (MIN, NY); Bradford Co., Brooker, *Dennison & Arnold s.n.* (FLAS); Citrus Co., Homosassa Springs, *Kral & Kral 6677* (GA, GH, NA, US, USF); Collier Co., Immokalee, *Lakela 30817* (DUKE, GH, TENN, USF); Columbia Co., Lake City, *Rolfs s.n.* (F, FLAS, GA); Dixie Co., Cross City, *Small s.n.* (GH, NCU, NY, USF); Duval Co., near Jacksonville, *Curtiss 4835* (E, FLAS, GA, GH, ISC, MIN, MO, MSC, NY, US); Gadsden Co., *Chapman s.n.* (NY); Gilchrist Co., 3 mi. E of Trenton, *Godfrey & Reinert 61087* (GH, LAF, SMU); Glades Co., 6.4 mi. SE of jct. of Fl. Hwys. 29 & 27 on 27, *Raven 18677* (MO); Hamilton Co., 2 mi. S of Genoa, *Arnold & West s.n.* (FLAS); Hardee Co., 7 mi. W of Sebring, *Sargent 7234* (FSU); Hernando Co., Lake Lindsey, *Godfrey 57284* (FSU, GH, USF); Highlands Co., Bootheel Creek, Venus, *Brass 20558* (NA, US); Hillsborough Co., Tampa, *Curtiss 934* (CM, F, FLAS, GH, KANU, MIN, MO, NY, US); Jackson Co., Jacksonville, *Curtiss 4835* (JE, W); Jefferson Co., Lloyds, *Nash 2509* (DAO, E, F, FLAS, G, GH, MIN, MO, MSC, NA, NCU, NEB, NY, US, VT); Lake Co., Eustis, *Nash 607* (E, F, GH, MO, MSU, NA, NY); Leon Co., Lake Bradford, *Godfrey 53654* (DUKE, FSU, GH, IA, NCU, NY, PAC, S, SMU, TENN, USF, VDB); Levy Co., Otter Creek, 1 mi. S of FL Hwy. 98, *Sargent 6230* (GA); Madison Co., 7 mi. W of Greensville, *Ramsey & Mitchell 14* (FSU); Manatee Co., 15 mi. E of Bradenton, *Genelle & Fleming 2002* (MO, USF); Marion Co., W of Dunnellon, *Janish et al. 329* (DS); Orange Co., 3 mi. S of Oakland, *Kral 7704* (FSU, GA, GH, IA, USF); Osceola Co., 6 mi. S of Kissimmee, *Arcuri & Richardson 861* (USF); Pasco Co., Jassamine, *Barnhart 2552* (F, MIN, NA, NY, US); Pinellas Co., Clearwater, *Fleming 167* (USF); Polk Co., Fort Meade, *Hood 4127* (FLAS); Putnam Co., Welaka, *Laessle s.n.* (FLAS); Seminole Co., Sanford, *Eaton 1048* (LL); Sumter Co., Withlacoochee State Forest, *Genelle & Fleming 2156* (USF); Suwannee Co., Liveoak, *Biltmore Herbarium 5966* (NA, US); Taylor Co., Shady Grove, *Godfrey & Kral 54946* (FSU, GA, GH, NY, SMU, TENN, USF); Union Co., Providence, *West & Arnold s.n.* (FLAS). **Georgia:** Bibb Co., Macon, *Bischoff s.n.* (MO); Chatham Co., Savannah, *Canby s.n.* (CM, F, GH, MICH, MO, NA, NCU, NMC, NY, US, VT); Decatur Co., 2 mi. E of Bainbridge, *Thorne 6154* (F, NA, NY, US); Echols Co., Mayday, Alapaha River, *Faircloth 6738* (GA, MO, NCU); Effington Co., Gayton to Springfield, *Harper 938* (MO, NA, NY, US); Jenkins Co., Jenkins Pond, *Duncan 5644* (GA); Lanier Co., 1.3 mi. W of Lakeland, *Faircloth 2651* (GA, NCU); Lowndes Co., Ocean Pond, *Faircloth 2331* (GA, NCU); Thomas Co., Ochlockonee River near Thomasville, *Small s.n.* (F, NA, NY, US). **South Carolina:** Aiken Co., Savannah River Operations Area of the Atomic Energy Commission, *Bateson & Kelley 79* (USCH); Allendale Co., 1.5 mi. NE of Milletville, *Radford et al. 11411* (BOON, CM, E, ECUH, FLAS, FSU, GA, MEXU, NCU, NO, NY, S, SMU, TENN, TEX, U, UNA, USCH, USF, VDB, WCUH); Barnwell Co., *Bateson & Kelley 33* (USCH); Beaufort Co., *Mellichamp s.n.* (NA); Charleston Co., Charleston, *Stewart s.n.* (F); Dorchester Co., Summerville, *Gibbs s.n.* (NY); Lexington Co., New Brookland, *Moore s.n.* (USCH); Richland Co., Columbia, *Taylor s.n.* (MICH).

4. **Ludwigia brevipes** (Long) Eames, Rhodora 35: 228. 1933. *Ludwigiantha brevipes* Long, in Britton & Brown, Ill. Fl. ed. 2. 2: 586. 1913. TYPE: U.S.A. New Jersey: Ocean Co., Long Beach Island [St. Alban's], moist open sand near Little Egg L. S. S., 20 Oct. 1907, *B. Long 173* (holotype, NY!; isotypes, GH!, PH!). Figures 1–3, 25.

Perennial herbs with prostrate stems, rooting at nodes, 20–70 cm long, sometimes forming large mats, erect or ascending at tips; usually minutely strigillose (the hairs 0.1–0.15 mm long) on leaf and sepal margins, capsules and pedicels, otherwise glabrous, occasionally glabrous throughout. Leaves oblanceolate-elliptic to narrowly oblanceolate, (7–)10–17(–20) × 2–7(–10.5) mm (those on submerged stems linear, 32–47 × 2.4–3 mm), apex acute, margin entire, base very narrowly cuneate or sometimes attenuate into narrowly winged petiole 2–8 mm long; stipules minute, reddish brown, ovate-lanceolate, 0.15–0.25 × 0.05–0.15 mm, succulent; bracteoles linear, 1–3(–4.5) × 0.12–0.65 mm, located at base of capsule or just below on upper pedicel. Flowers in leaf axils, usually in a few-flowered spike; sepals triangular to narrowly triangular (3.5–)4–5(–5.8) × 1.7–2.8 mm, with 3 parallel veins, slightly reflexed at anthesis, ascending in fruit, apex very narrowly acute or elongate acuminate; petals yellow, oblong-spatulate, 4.5–5.2 × 1.5–2.5 mm, apex obtuse, base attenuate; anthers 0.75–1 mm long; filaments 1.8–2.5 mm long; pollen shed in very loose tetrads; nectary disc bright yellow, raised 0.55–0.7 mm on ovary summit, 1.7–2.3 mm across, 4-lobed; style 1.1–1.7 mm long; stigma 0.4–0.55 mm long, 0.55–0.8 mm thick. Capsules clavate, sometimes slightly curved, 6–10.5 mm long, (2–)2.5–4 mm thick, glabrous to minutely strigillose or with very minute erect protuberances 0.04–0.06 mm long, pedicels (4.5–)6–15(–20) mm long. Seeds

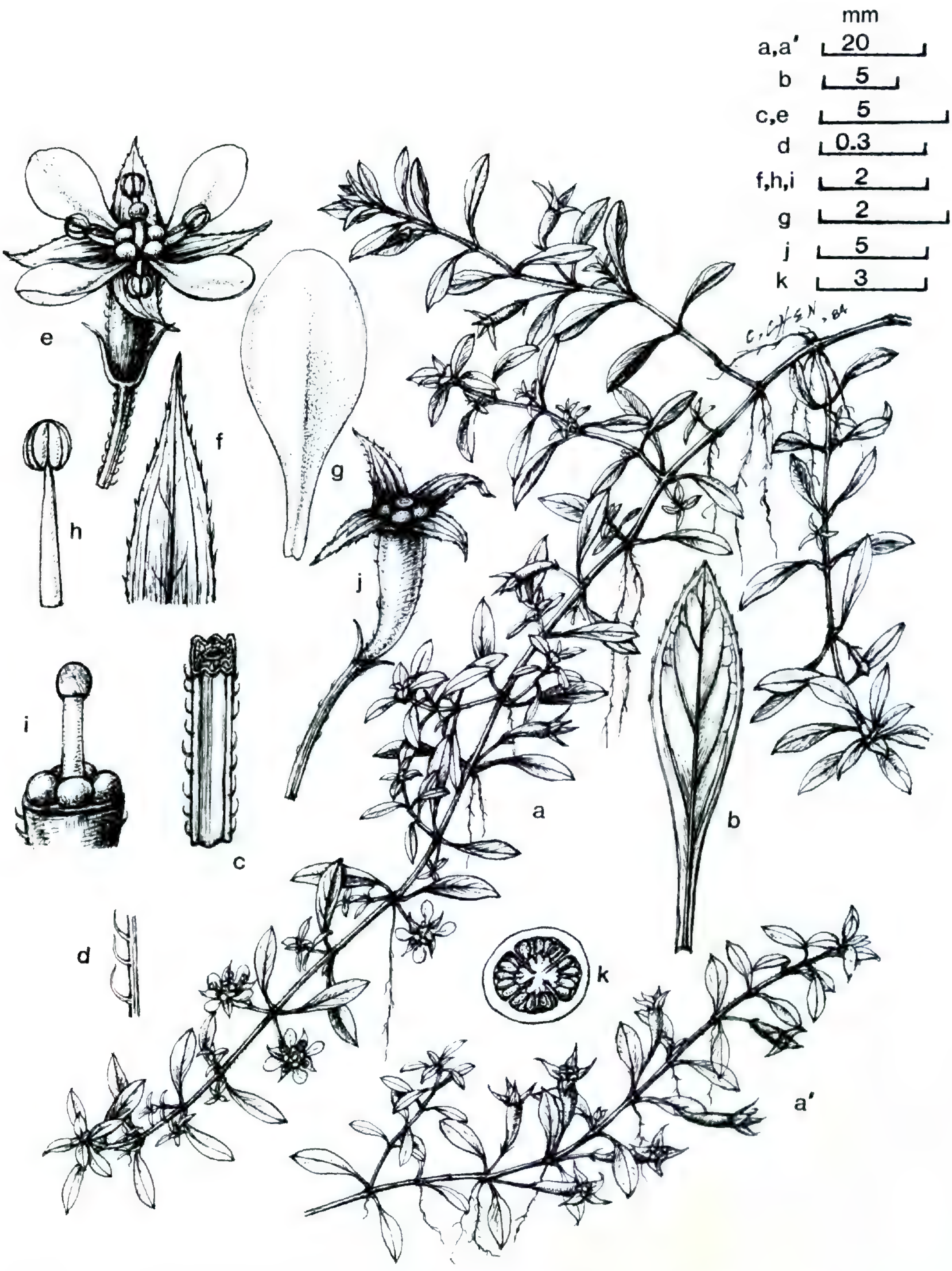

Figure 25. *Ludwigia brevipes*; New Jersey, Ocean Co., *Long 462* (NY). —a, a′. Habit. —b. Leaf. —c. Portion of stem. —d. Strigillose hairs on stem. —e. Flower. —f. Sepal. —g. Petal. —h. Stamen. —i. Dissected flower showing stigma, style, nectary disc, and upper ovary. —j. Fruit. —k. Fruit, cross section.

light to dark brown, ellipsoid, 0.65–0.7 × 0.35–0.45 mm, surface cells transversely elongate. Self-compatible. Gametic chromosome number, $n = 24$.

Phenology. Flowering from June to September; fruiting from June to October.

Distribution (Fig. 22). *Ludwigia brevipes* is restricted to the Coastal Plain of the United States, ranging from central and eastern South Carolina northeastward through eastern North Carolina to extreme southeastern Virginia. The type collection of *L. brevipes* from middle New Jersey remains the only disjunct population north of the main range of this species 80 years after it was found. More recently, in 1988, an isolated population (*Burkhalter 11065*) well to the southwest of the main range of *L. brevipes* was discovered in the panhandle of Florida (Fig. 22). Previous records of *L. brevipes* from peninsular Florida, however, were erroneous and based on natural hybrids between *L. arcuata* and *L. repens* (Fig. 4; see discussion under Sympatric Occurrence and Natural Hybridization).

Habitat. Plants of *L. brevipes* grow on wet soil or moist sand along the borders of ponds, lakes, or marshes, and riverbanks. They are also found in wet sand of dune hollows or along peaty margins of coves. In North Carolina, most collections are from habitats inundated in wet seasons and exposed in dry seasons (Duke, 1955).

Ludwigia brevipes, together with the more widespread *L. repens*, constitute the hexaploids in the section. Although the two species are quite distinct in morphology, they are interfertile and form complete chromosome pairings at meiosis in artificial hybrids. *Duke 54–243* (North Carolina, Dare Co.) appears to be a natural hybrid of this combination.

Ludwigia brevipes also hybridizes with the widespread diploid *L. palustris*. Such hybrids are found not only in North Carolina and southeastern Virginia where both parental species occur, but also as far north as Connecticut and Rhode Island, and south in Jenkins Co., Georgia, in both cases outside the normal range of *L. brevipes* (Fig. 5). Unlike the homoploid hybrid between *L. brevipes* and *L. repens*, these hybrids are highly sterile. They are robust plants, however, and reproduce vigorously by vegetative means. Hybrids of this combination were given specific status as *L. lacustris* by Eames (1933).

Ludwigia brevipes is a hexaploid with three different genomes (AABBCC). Biosystematic analysis suggests that the AA genome may have been derived from the diploid *L. palustris* and the BB and CC genomes from the tetraploid *L. arcuata*. Artificial hybrids between *L. palustris* and *L. arcuata* (Fig. 6) are morphologically similar to *L. brevipes*.

Representative specimens examined. NORTH AMERICA. U.S.A. **Florida:** Escambia Co., SW of Pensacola, *Burkhalter 11065* (FSU, HAST, MO, UWFP). **New Jersey:** Ocean Co., Little Egg L. S. S., Long Beach Island, *Long 173* (GH, NY, PH; type collection). **North Carolina:** Columbus Co., Lake Waccamaw, *Matthews s.n.* (DUKE); Craven Co., New Bern, *s.c. s.n.* (NY); Currituck Co., road to Mackay's Island, *Radford 5445* (NCU); Dare Co., Kill Devil Hills, *Fox & Godfrey 4445* (B, BH, CAS, DS, FSU, GA, GH, IA, ISC, NY, OKLA, PAC, PENN, S, SMU, TEX, US, WIS, WVA); Gates Co., NE of Gatesville, *Ahles & Duke 48466* (DAO, FSU, G, GA, GH, NCU, NY, USF, VDB); Harnett Co., S of Bunnlevel, *Raven 18101* (DS); Hyde Co., 2 mi. W of Lake Landing, Lake Mattamuskeet, *Hotchkiss & Ekvall 3745* (US); Johnston Co., Holt's Lake, 4 mi. S of Smithfield, *Whiteford 256* (NCSC); Pasquotank Co., 12 mi. NW of Elizabeth City, *Godfrey 5247* (GH, NA, US); Robeson Co., 3 mi. NW of Lumberton, *Fox 5573* (FLAS, GA, MIN, NCSC, NY, TENN); Sampson Co., 2 mi. W of Salemburg, *Beal 3624* (NCSC); Wayne Co., 4 mi. E of Mt. Olive, *Beal 3281* (DUKE, NCSC). **South Carolina:** Horry Co., Waccamaw River, N of Little River, *Duke 54–117* (NCU); Lee Co., Mechanicsville, *Radford 24066* (CA, COLO, KANU, NCU, OKLA); Lexington Co., Columbia, *Godfrey & Tryon 1195* (CU, DUKE, F, GH, MO, NY, US). **Virginia:** Isle of Wright Co., Cat Pond, S of Benns Church, *Fernald & Long 8376* (F, GH, NY); Norfolk Co., James River, Portsmouth, *Rugel s.n.* (GH); Princess Anne Co., Chesapeake Beach, *Fernald et al. 15324* (GA, GH, MO, NY, TENN, US); Southampton Co., Whitefield's Millpond, SW of Corinth, *Fernald et al. 15323* (B, GH, NA, NY, S, SMU, US).

5. Ludwigia repens J. R. Forst., Fl. Amer. Sep. 6. 1771. TYPE (typ. cons. Reveal et al., Taxon 52: 864. 2003; Brummit, Taxon 54: 533. 2005): U.S.A. Florida: Duval Co., swamps and ditches near Jacksonville, 19 May 1894, *A. H. Curtiss 4836* (neotype, designated by Reveal et al. (2003: 864), MO!; isotypes, FLAS!, GA!, GH!, MSC!, NA!, NY!, P!, W!). Figures 1–3, 26.

Ludwigia repens Swartz, Nov. Gen. Sp. Pl. Prodr. 33. 1788, nom. superfl., non *Ludwigia repens* J. R. Forst., 1771. *Isnardia repens* (Swartz) DC., Prodr. 3: 60. 1828. TYPE: Jamaica, s.d., *O. Swartz s.n.* (holotype, S!; isotype, C!).

Ludwigia natans Elliott, Sketch Bot. S. C. & Ga. 1: 581. 1821. *Isnardia natans* (Elliott) Kuntze, Rev. Gen. Pl. 1: 251. 1891. TYPE: U.S.A. South Carolina: Barnwell Co., in small running streams, in Barnwell district, near the Court House, s.d., *S. Elliott s.n.* (holotype, CHARL!; photo of holotype, GH!, MO!, NY!).

Ludwigia fluitans Scheele, Linnaea 21: 580. 1848. TYPE: U.S.A. Texas: Comal Co., in clear, flowing water, Comal Spring, in masses together, Aug. 1846, *F. Lindheimer [Fasc. III.] 395* (lectotype, designated here, MO!; isotypes, MO [2]!, US!).

Ludwigia natans Elliott var. *rotundata* (Griseb.) Fernald & Griscom, Rhodora 37: 175. 1935. *Isnardia repens* (Swartz) DC. var. *rotundata* Griseb., Cat. Pl. Cub.

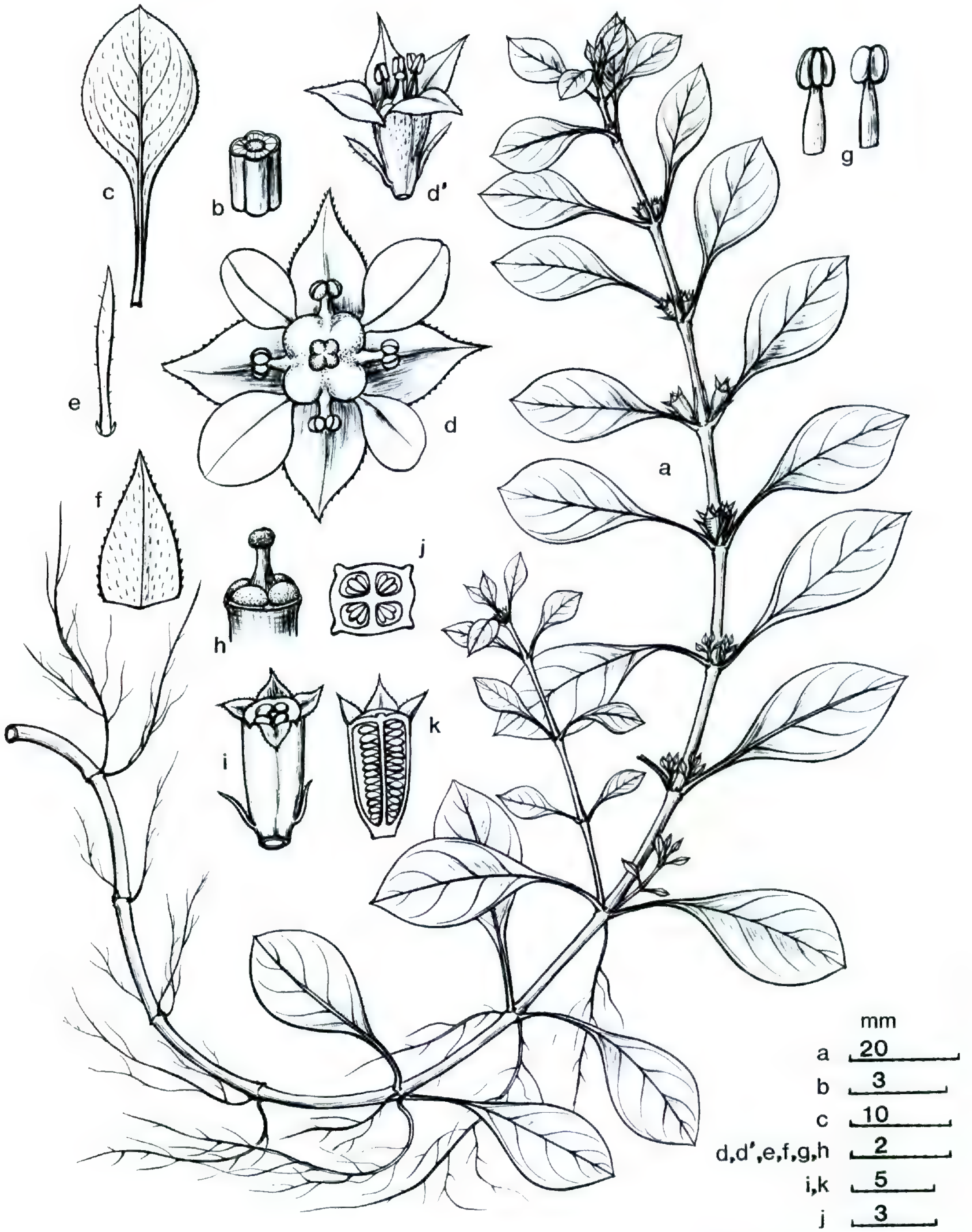

Figure 26. *Ludwigia repens*; Florida, Lee Co., *Peng et al. 4291* (MO). —a. Habit. —b. Portion of the stem. —c. Leaf. —d. Flower, top view. —d'. Flower, lateral view, petals removed. —e. Bracteole. —f. Sepal. —g. Stamen, adaxial and abaxial view. —h. Partly dissected flower showing stigma, style, disc, and upper ovary. —i. Fruit. —j. Fruit, cross section. —k. Fruit, longitudinal section.

107. 1866. *Ludwigia repens* Swartz β *rotundata* (Griseb.) M. Gómez, Anales Soc. Esp. Hist. Nat. 23: 66. 1894. TYPE: Cuba. *C. Wright 2553* (holotype, GOET!; isotypes, G!, GH!).

Isnardia intermedia Small & Alexander, in Small, Man. SE. Fl. 940, 1506 (as "*media*"). 1933. TYPE: U.S.A. Florida: Dade Co., Everglades, NW of Perrine, Hammock Islands, betw. Homestead & Cross Key, 1906, *J. Small & J. Carter 2626* (holotype, NY!; isotypes, SMU!, TENN!).

Ludwigia repens J. R. Forst. var. *stipitata* (Fernald & Griscom) Munz, N. Amer. Fl. II. 5: 53. 1965. *Ludwigia*

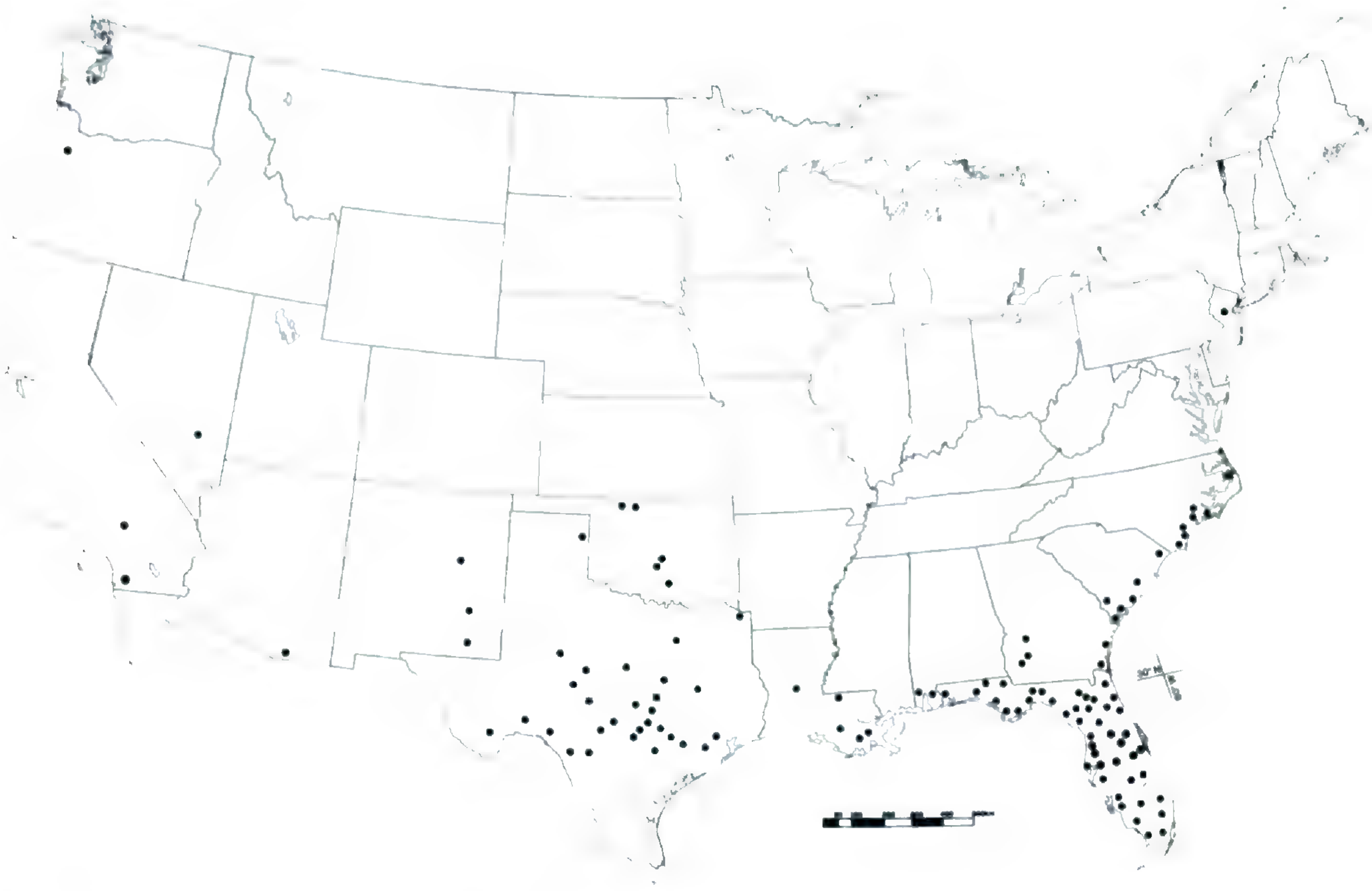

Figure 27. Distribution of *Ludwigia repens* in the U.S.A.

natans Elliott var. *stipitata* Fernald & Griscom, Rhodora 37: 175. 1935. TYPE: U.S.A. California: San Bernardino Co., Jan. 1880, *S. Parish & W. Parish 682* (holotype, GH!; isotypes, DS!, F!, MO[2]!).

Perennial herbs with prostrate stems, rooting at nodes, the tips ascending or suberect, glabrous or nearly so. Leaves lustrous, usually dark green adaxially and purplish green abaxially, or sometimes purplish green on both surfaces, narrowly elliptic to broadly lanceolate-elliptic or suborbicular, blades 8–45 × 4–27 mm, nearly glabrous, apex acute or apiculate, rarely obtuse, margin entire or with minute, obscure hydathodal teeth, sparingly to densely finely papillose-strigillose, the hairs ca. 0.05–0.1 mm long, base attenuate into narrowly winged petiole 3–23 mm long; stipules minute, reddish purple, lanceolate to deltoid, 0.15–0.3 × 0.1–0.3 mm; bracteoles lanceolate or narrowly oblong-lanceolate, 1–5(–8) × 0.1–1 mm, sparingly minutely strigillose, attached 1–3(–5) mm below base of capsule. Flowers axillary and paired; sepals green, ovate-deltate to narrowly so, 1.8–5 × 1.5–3.5 mm, ascending, nearly glabrous, apex acuminate to elongate acuminate, margin minutely papillose-strigillose, the hairs ca. 0.05 mm long; petals yellow, oblanceolate to elliptic-oblong, 1.1–3 × 0.25–1.4 mm, apex obtuse, base attenuate, often variable in size and shape in the same flower; anthers 0.4–0.9 mm long and wide; filaments pale yellow, 0.5–1.5 mm long; pollen shed singly or in tetrads; nectary disc yellow, raised 0.3–0.8 mm on ovary summit, 1.1–3 mm across, 4-lobed, glabrous; style pale yellow, 0.6–0.9 mm long, glabrous; stigma pale yellow, 0.3–0.45 mm long, 0.3–0.8 mm thick. Capsules dark green (brown upon drying), elongate obpyramidal or oblong with attenuated base, the corners rounded or barely angled, 4–10 mm long, 2.5–4 mm thick, glabrous to sparingly short puberulent or finely strigillose, the hairs 0.05–0.1 mm long, subsessile or with pedicels up to 3 mm long. Seeds yellowish brown, ellipsoid, 0.6–0.8 × 0.3–0.45 mm, surface cells transversely elongate. Self-compatible. Gametic chromosome number, $n = 16$.

Phenology. Flowering and fruiting all through the year, or in cooler climates throughout the growing season.

Distribution (Figs. 27, 28). *Ludwigia repens* occurs primarily on the Atlantic and Gulf Coastal Plains of the United States, from North Carolina south through Florida, and west to Texas and northeastern Mexico (Nuevo León), with outlier populations in New Jersey, Oklahoma, southern Arizona, New Mexico, Nevada, California, and Oregon. It also is widespread in the savannas of central Texas and the Edwards Plateau region, extending southwest into the Mexican states of Nuevo León, Coahuila, Chihuahua, and Sonora, and south into San Luis Potosí, México, Morelos, and Puebla. *Ludwigia repens* also occurs in the Caribbean region, including Cuba, Haiti, Dominican Republic, the Ba-

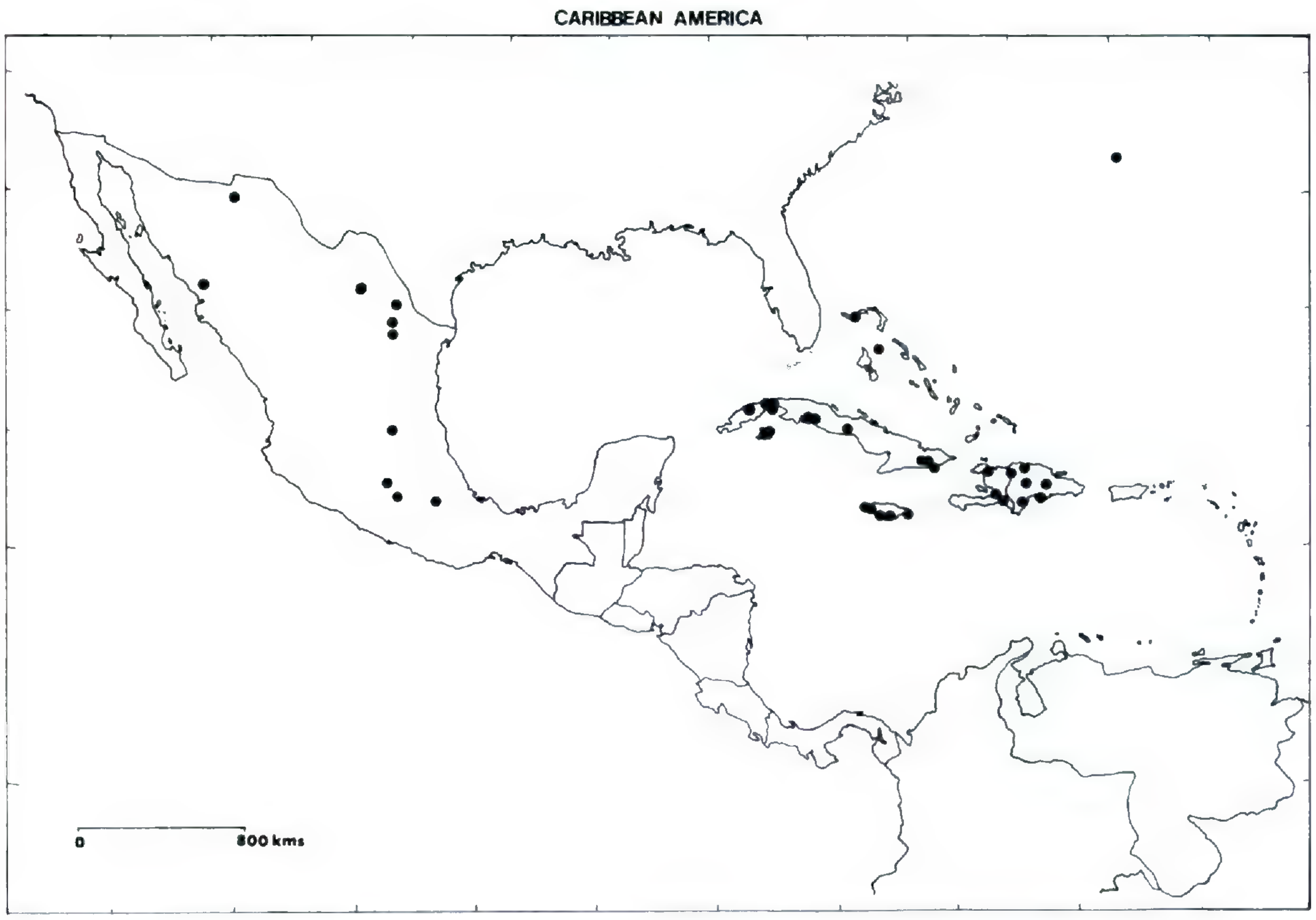

Figure 28. Distribution of *Ludwigia repens* in Central America and the Caribbean region.

hamas, and Bermuda. Although *L. repens* is considered endangered in Missouri (Wilson, 1984) based on a record from Greene County (Steyermark, 1963; as *L. natans* Ell.), we could not locate a voucher specimen to verify this report. Recently, *L. repens* has become naturalized in Bangladesh (Khan, 1977) and Japan (Murata & Peng, 1988).

Habitat. Plants of *Ludwigia repens* grow on muddy or sandy borders of pools, lakes, and swamps; along creek or riverbanks and commonly in roadside ditches; in moist soil in solution pits in limerock and hammock clearings in the Everglades of Florida; in open, sunny places or partial shade. They occur most often in coastal lowlands, but can be found at higher elevations, e.g., to ca. 600 m in Kerr County, Texas, 850 m in San Bernardino County, California, 1150 m in Chaves County, New Mexico, and 1500 m in Puebla State, Mexico.

As detailed by Raven (1965) and Reveal et al. (2003), Forster described *Ludwigia repens* based on an earlier description by Clayton in Gronovius's *Flora Virginica* (ed. 2: 20. 1762), a work that did not adopt the binomial system of nomenclature. However, Forster designated a specimen (*Clayton 775* from Virginia) that is clearly synonymous with *Ludwigia palustris*. Following Raven's (1965) resurrection of the Forster name, it has been taken up universally in both systematic and non-systematic literature for the present taxon, in place of *L. natans* Elliott (1821). In order to avoid a disadvantageous nomenclatural change for this widespread taxon, Reveal et al. (2003) proposed a neotype that maintains current usage; this proposal was approved by the Committee for Spermatophyta (Brummit, 2005).

Regarding typification of *Ludwigia fluitans* Scheele, no specimens of *Lindheimer 395* could be located that Scheele clearly had in his possession. Instead we have chosen as lectotype a specimen at MO, the home institution of Engelmann, who distributed Lindheimer's collections. The MO specimen includes an annotation (not in Engelmann's handwriting) of "*Ludwigia fluitans* Scheele."

Like *Ludwigia palustris*, *L. repens* is widespread and variable, mainly in shape and size of leaves, flower and capsule size, bracteole and pedicel length, and tightness of pollen tetrads. Emphasizing differences in capsule size and pedicel length, Fernald and Griscom (1935) described three varieties of this species, two of them restricted to the east coast of the United States. Duke (1955: 266) noted that "occasionally a plant will have capsules varying from 3 to 7 mm in length, with the smaller fruits being mostly on branches; often accompanying this variation is a proportionate variation in bracteole length." As with *L. palustris*, much of the variation

may have to do with with the environments in which these plants occur. The varieties proposed for *L. repens* by Fernald and Griscom (1935) are, as suggested by Duke (1955) and later by Munz (1965), ill-defined in many respects, and variation within each is so great as to make them not worthy of recognition.

The range of *Ludwigia repens* overlaps with all other species in section *Dantia*. *Ludwigia repens* forms natural hybrids with *L. brevipes* (see discussion under *L. brevipes*), *L. arcuata* (see discussion under *L. arcuata*), and *L. palustris*.

Ludwigia repens frequently co-occurs with *L. palustris* in the field, and natural hybrids are found scattered in Florida, North Carolina, Great Bahama, and Mexico. Like both putative parents, the hybrids are highly variable in morphology, especially in leaf shape. The hybrids also have a variable number (0 to 4) of vestigial petals. The ovaries are oblong-obpyramidal like those of *L. repens* but somewhat smaller, and these typically abort after anthesis. The percentage of stainable pollen is usually very low, less than 10%. The most diagnostic characters for these hybrids in fact are abortive capsules and/or very sterile pollen. Because their morphology is intermediate between that of two variable species, these hybrids would be difficult to identify without flowers and fruits, which they commonly lack in their aquatic or semiaquatic habitats.

Representative specimens examined. NORTH AMERICA. MEXICO. **Chihuahua:** valley of the Rio Grande, below Doñana, *Thurber 8131* (F, GH, NY). **Coahuila:** Los Fresnos Laguna, *Pinkava et al. 4302* (MO). **México:** 20 km NW of Cuernavaca, *Fassett 28441* (F, G, GH, MEXU, MICH, WISC). **Morelos:** 2 mi. N of Alpuyeca, *Quiram 52* (MEXU). **Nuevo León:** Ojo de Aqua at El Nogador, 5 mi. N of Monterrey, *Corzo & Koerdell 14586* (ENCB, F, GH, MO, NY, TEX, US). **Puebla:** San Gabriel Chilac near San Juan Atzingo and San Andrés, *Smith et al. 4100* (F, GH, MEXU, NA, NY, TEX). **San Luis Potosí:** Tamasopo, Agua Buena, *Gray 16* (MO). **Sonora:** Canyon Estrella, Dist. Alamos, *Gentry 419* (DS). U.S.A. **Alabama:** Baldwin Co., Romar Beach, *Kral 38210* (VDB); Mobile Co., Lackland, *Deramus D678* (NCU). **Arizona:** Santa Cruz Co., Monkey Springs, ca. 6 mi. N of Patagonia, *Correll & Correll 39285* (LL, NY). **California:** San Bernardino Co., Mohave River at Victorville, *Wheeler 2063* (DS, F, G, GH, MO, ND-G, NY, TEX); San Diego Co., *Vasey s.n.* (F, G, GH). **Florida:** Alachua Co., Poe Springs Run, High Springs, *Swindale & Judd 1227* (MO); Bay Co., Tyndall AF Base, Felix Lake to Freshwater Bayou, *Perkins & Nelson 447* (FLAS); Bradford Co., 3.5 mi. NW of Starke, *Wiggins 19993* (USF); Brevard Co., St. John's River bridge W of Melborne, *Lakela 27190* (DS, FLAS, GH, NY, SMU); Broward Co., 2.5 mi. W of St. John's River, *Wooten 2237* (NCU); Charlotte Co., Port Charlotte, *Godfrey & Reinert 60964* (NCU); Citrus Co., Banana Island, *Hartman & Ward 32* (FLAS); Collier Co., Turner's River Hammock, *Moldenke 671* (DUKE, NA, NY, S, W); Columbia Co., Itchatucknee Springs, *Swindale 1219* (NCU); Dade Co., between Cutler and Longview Camp, *Small & Carter 838* (NCU); Dixie Co., 4 mi. NW of Cross City, *Godfrey 56020* (LL, MEXU, NCU, VDB); Duval Co., near Jacksonville, *Curtiss 4836* (FLAS, GA, GH, MO, MSC, NA, NY, P, W; neotype); Escambia Co., W end of Santa Rosa Island, *Burkhalter 5311* (FLAS); Flagler Co., Bunnell, *West & Arnold s.n.* (FLAS); Franklin Co., Apalachicola, *Chapman s.n.* (GH); Gilchrist Co., Hart Springs, *West & Arnold s.n.* (FLAS); Gulf Co., Dead Lake, Wewahilchka, *Demaree 50430* (NO, SMU, VDB); Hendry Co., 3 mi. S of Labelle, *Henderson 63–1610* (TEX); Hernando Co., 3 mi. W of Weeki Wachee Springs, *Kral & Kral 7028* (FLAS, GA, RSA); Highlands Co., Parker Islands, 3 mi. S of Klae Istokpoga, *Brass 15295* (FLAS, G, NA); Hillsborough Co., E of Temple Terrace, *Lakela 24844* (FLAS); Holmes Co., Ponce de Leon, *Demaree 57773* (GA, VDB); Jackson Co., Blue Springs, *Thorne & Davidson 16656* (F, G); Jefferson Co., Wacissa River, *Godfrey 73679* (FSU); Lake Co., Eustis, *Nash 2134* (G, MSC, MO, NA, ND-G, NY); Lee Co., Ft. Myers, *Standley 242* (F, G, MO, NA, NY); Leon Co., St. Marks, *Rugel s.n.* (MO, NW, W); Levy Co., *Cooley & Eaton 6532* (FLAS, NCU, TEX); Manatee Co., Bradenton, *Tracy 7592* (CM, G, F, MO, MSC, NA, NCU, NY, SMU, TAES, W); Marion Co., Juniper Springs Creek, *Hansen & Richardson 5436* (USF); Martin Co., Dickenson State Park, *Popenoe & Roberts 1261* (FTG); Monroe Co., Pine Crest, *Moldenke 864* (DUKE, S); Okeechobee Co., mouth of Kissimmee River, *Small & Small 4386* (G, NA, NCU, NY); Orange Co., Lake Tsala Apopka, Floral City, *Kalela 24902* (MO); Osceola Co., along U.S. Hwy. 192, *Stone 1650* (DUKE); Palm Beach Co., 2 mi. W of Lake Worth, *McCart 9516* (FLAS, NCU); Pasco Co., Aripeka, *Kral 7305* (FLAS, G, GA, NA, RSA, VDB); Pinellas Co., 4 mi. E of Clearwater, *Kral 7453* (G, RSA, VDB); Polk Co., Loughman, *McFarlin 5733* (FLAS); Putnam Co., Cabbage Creek, *Nelson 676* (FLAS); St. Johns Co., St. Augustine, *West & Arnold s.n.* (FLAS); Seminole Co., 2 mi. E of Geneva, *Kral 5100* (G, MSU); Taylor Co., Salem, *Demaree 52753A* (SMU, VDB); Union Co., Olustee Creek, *West & Arnold s.n.* (FLAS); Wakulla Co., 0.7 mi. from St. Mark's Light House, *Morar 14* (DUKE, SMU); Walton Co., 4 mi. NE of Knox Hill, *Wilhelm 9741* (USF). **Georgia:** Baker Co., Big Cypruss Creek, *Thorne 1564* (GA, TENN); Camden Co., 6.6 mi. S of Woodbine, *Raven 18702* (MO); Dougherty Co., Albany, *Pollard & Maxon 526* (NA, NY); McIntosh Co., Sapelo Island, *Duncan 20181* (CAS, DUKE, F, G, GA, MISS, NCU, SMU, TEX); Sumter Co., Leslie, *Harper 426* (MO, NA, NY, W). **Louisiana:** Assumption Parish, 9 mi. E of Morgan City, *Thieret 25729* (DS, DUKE); Jefferson Parish, Black Bayou, *Ewan 21005* (DS, NO); Lafourche Parish, Raceland, 8 Oct. 1939, *s.c. s.n.* (NO); Rapides Parish, Alexandria, *Hale s.n.* (NY). **Nevada:** Lincoln Co., Crystal Springs, *Tiehm 3443* (MO, NY, UNA). **New Jersey:** Somerset, *Moldenke 1349a* (W). **New Mexico:** Chaves Co., Roswell, *Earle & Earle 334* (MO, NA, NY, POM, W); Eddy Co., Rattle Snake Spring, Lincoln Nat'l. Forest, *Crutchfield 751* (LL); Guadalupe Co., James Wallace Park, *Crutchfield 1863* (LL). **North Carolina:** Brunswick Co., Rattlesnake Branch, 3 mi. W of Winnabow, *Radford 5806* (FSU, GA, NA); Carteret Co., SE of Mullet Pond, *Anderson 410* (DUKE, SMU); Dare Co., Cape Hatteras, *Ashe s.n.* (NCU); Jones Co., 1.5 mi. NE of Pollocksville, *Radford et al. 7329* (G, GA, NCU); New Hanover Co., Mockingbird Lane, Winter Park, *McCrary 844* (NCU); Onslow Co., White Oak River, *Boufford et al. 21568* (MO); Pender Co., 4 mi. WNW of Hampstead, *Beal 2387* (NCU). **Oklahoma:** Alfalfa Co., OK

Hwy. 9 S of Carmen Rd., *Correll & Correll 39075* (LL, NY); Cleveland Co., Canadian River, SW of Norman, *Bradley 1447* (MO); McClain Co., 4 mi. SW of Norman, *Barkley s.n.* (DS); Murray Co., SE of Hennepin, *Waterfall 6109* (DS, MO, NY); Woods Co., *White 232* (MO). **Oregon:** Marion Co., Salem, *Hall 1911* (F). **South Carolina:** Beaufort Co., near Trichinham Plantation, *Bell & Ahles 15560* (NCU); Berkeley Co., Santee Canal, NW of Bonneau, *Godfrey & Tryon 481* (F, G, MO, NA, NY, POM); Charleston Co., Francis Marion Nat'l. Forest, *Evans et al. 4030* (TENN); Hampton Co., Coosawhatchie River near Luray, *Eyles 6471* (GA); Horry Co., Myrtle Beach, *Godfrey & Tryon 1171* (CAS, F, G, MO, NA, NY, POM). **Texas:** Bandera Co., E of the Sabinal River, *Smith 598* (LL); Bell Co., Little River, *Wolff 2221* (NA, SMU, TAES); Bowie Co., 6 mi. N of Avery, *Correll 34427* (LL); Brewster Co., 15 mi. S of Marathon, *Whitehouse 18662* (SMU); Burnet Co., 8 mi. E of Marble Falls, *Crutchfield 816* (LL); Colorado Co., Eagle Lake, *Barkley et al. 46459* (TEX); Comal Co., Comal Springs at New Braunfels, *Correll & Crutchfield 31060* (LL); Comanche Co., Comanche Springs, New Braunfels, *Lindheimer 807* (F, G, M, MO, NA, NY, TEX, W); Dallas Co., Dallas, *Hall 223* (F, MO, NY); Fayette Co., *Matthes 156* (W); Fort Bend Co., 5.6 mi. NW of Arcola, *Raven & Gregory 19402* (MO); Gillespie Co., 10.25 mi. NE of Kerrville, *Cory 32340* (G); Gonzales Co., Ottline, *Bogusch 1522* (TEX); Harris Co., Houston, *Lindheimer s.n.* (MO); Hays Co., San Marcos, *McCart 5817* (SMU); Hemphill Co., 5 mi. E of Canadian, *Higgins 12291* (NY); Kendell Co., E of Boerne, *Ertter 5467* (MO); Kerr Co., Kerville, *Heller 1887* (F, G, MO, MSC, NA, NY, POM, SMU); Kinney Co., 22 mi. E of Del Rio, *Kral 21198* (DS, VDB); Leon Co., *Tharp s.n.* (CAS); McLennan Co., *Smith 917* (TEX); Menard Co., 11 mi. W of Menard, *Tilton & McCart 5828* (SMU); Mitchell Co., Hackberry Creek, *Pohl 4649* (SMU); Pecos Co., Comanche Springs, Ft. Stockton, *Warnock 8861* (SR); Runnels Co., 10 mi. E of Ballinger, *Cory 43669* (TEX); Terrell Co., 7 mi. from jct. of Independence Creek and Pecos River, *Webster 497* (LIL, TEX, UNA); Tom Green Co., Christoval, S Concho River, *Wolff 4204* (SMU); Travis Co., Barton Springs Creek, *Barkley 13369* (F, MO, NA, NY, TEX); Uvalde Co., 12 mi. SE of Uvalde, *Cory 23868* (G); Val Verde Co., Del Rio, *Cole et al. 3501* (NY, USF); Williamson Co., 3 mi. W of Taylor, *Walker 85* (SMU, TEX).

CARIBBEAN. BAHAMAS. **Grand Bahama:** Eight Mile Rock, *Correll & Kral 43084* (F, G, LL, NY, VDB). **New Providence:** Farringdon Rd., *Britton & Brace 200* (F, GH, NY, US). BERMUDA. Devonshire Marsh, *Brown & Britton 91* (F, G, GH, NA, NY, US). CUBA. **Ciego de Avila:** Soledad, *Gonzales 12* (A, FLAS, GH, NY, S, U). **Cienfuegos:** La Magdalena, *Baker 2478* (F, G, MIN, NY, POM, US). **Guantanamo:** Monte Verde, *Shafer 8716* (F, GH, NY, U, US). **Ilsa de la Juventud:** Jucaro, *Britton et al. 14623* (F, NA, NY). **La Habana:** Laguna de Ariguanabo, *Léon 10617* (GH, NY, US). **Matanzas:** Canal del Roque, Circuito Norte, *Alain 3910* (GH, US). **Pinar del Rio:** San Diego de los Baños, *Britton et al. 6905* (NY). **Santiago de Cuba:** La Perla, *Shafer 8725* (GH, NY, US). DOMINICAN REPUBLIC. **Baoruco:** Puerto Escondido, *Howard 12138* (A, DUKE, GH, MEXU, RSA). **Barahona:** Cabral, *Fuertes 867* (F, G, GH, MIN, MO, NA, S, U, Z). **Dajabon:** Rio de las Carilas, Partido, *Liogier 16280* (G, NY). **La Vega:** Cordillera Central, Constanza, *Ekman 13916* (S). **Peravia:** Bani, El Corbanal, *Alain & Liogier 22397* (NY), *Lavastre 2304* (NY). **Puerto Plata:** El Choco, W of Cabarete, *Liogier 16507* (NA, NY). **San Cristobal:** Bayaguana, *Liogier & Liogier 19008* (F, NY). HAITI. **Nord:** Bayeux, Port Margot, *Nash & Taylor 1213* (NY). **Ouest:** Port-au-Prince, *Ekman 5662* (G, LL, NY, S). Province unknown: Bassin Bleu, *Leonard & Leonard 14892* (G, NA, NY). JAMAICA. **Clarendon:** Cockpit River S of pumping station, *Proctor 37200* (FTG, MO). **St. Elizabeth:** Styx River, Slipe District, *Proctor 24740* (DUKE, F, G, MO). **St. Thomas:** Morant River, *Proctor 31575* (LL, U). **Westmoreland:** 0.75 mi. SSW of Petersfield, *Proctor & Mullings 22031* (G, GH, LL, NY).

Interspecific Hybrids

In this section, we present data for all known hybrids among species of *Ludwigia* sect. *Dantia*. Formal names have been proposed for only one hybrid combination, which is listed first; other hybrids are listed alphabetically. Chromosome numbers of the putative parents are indicated in parentheses after their names.

Ludwigia brevipes ($n = 24$) × **L. palustris** ($n = 8$)

Ludwigia ×lacustris Eames, pro sp., Rhodora 35: 228. 1933. TYPE: U.S.A. Rhode Island: Washington Co., Charlestown, in moist pure sand on long-emersed beach at Watchuag Pond, 12 Sep. 1932, *E. H. Eames 11498* (holotype, GH!).

Ludwigia ×lacustris Eames f. *aquatilis* Eames, pro sp., Rhodora 35: 229. 1933. TYPE: U.S.A. Connecticut: New Haven Co., N Branford, in Little West Pond; Guilford, West Pond, 22 Aug. 1932, *E. H. Eames 11475* (holotype, GH!; isotype, PH!).

Eames (1933) described *Ludwigia lacustris* as a new species, apparently unaware that his collection represented a natural hybrid between the hexaploid *Ludwigia brevipes* and the diploid *L. palustris*. In the same article, he also described *L. lacustris* forma *aquatilis*, which is "a submerged form of peculiar characteristics" (Eames, 1933: 227). Based on collections from Connecticut and Rhode Island, Eames in his protologue remarked that the new species and new forma were similar to *L. brevipes*, differing mainly in the smaller flowers (5.5–6.5 mm vs. 12–13 mm across), pedicels (1–2.5 mm vs. 5–12 mm long), ovaries (2–3 mm vs. 4–6 mm long), sepals (2.5–3 mm vs. 4–6 mm long), and petals (1.3–3 mm vs. 4–6 mm long). He also noted, "after flowering the sepals and ovary grow a little longer and, unless fertilized (which is rarely, or late), becomes yellow, contract and drop off with sepals expanded" (Eames, 1933: 229); however, he did not specifically consider the possibility that the plants were hybrids.

Analysis of experimental hybrids shows that, like all species of section *Dantia*, this hybrid is capable

of undergoing mechanical self-pollination, but the pollen is unable to effect fertilization. The pollen of *Ludwigia ×lacustris* is only about 10% viable, a figure comparable to that of artificial hybrids between *L. palustris* and *L. brevipes* (4%–12%; Table 4).

Cytological analysis of putative hybrids from Connecticut (*Raven 16518*, DS) and North Carolina (*Ornduff 6461–2*, UC) shows 8 bivalents and 16 univalents in meiosis (Schmidt, 1967: fig. 3), a result in agreement with that of an artificial hybrid between *L. brevipes* and *L. palustris* (Fig. 16). Based on cytological analysis of the specimen from Connecticut (near the type locality of forma *aquatilis*) in the unpublished dissertation of Schmidt (1967), Raven and Tai (1979) first reported the hybridity of *L. ×lacustris*, but described it as a sterile triploid hybrid. Clearly, however, the hybrid is tetraploid.

Eames (1933) described *Ludwigia ×lacustris* as petaliferous, but some individuals of this hybrid combination, e.g., *Ornduff 6461-2* (North Carolina, Johnston Co.) and *Duncan 5645* (Georgia, Jenkins Co.), lack petals, and stamens often appear in the position of the petal, even appearing petaloid.

Although *Ludwigia brevipes* has a fairly limited distribution (Fig. 22), in several localities it apparently has formed natural hybrids with the widespread *L. palustris*. These hybrids are widely scattered along the Atlantic Coastal Plain (Fig. 5), including localities outside the current range of *L. brevipes*. The documented range of *L. brevipes* extends as far north as middle New Jersey, some 240 km south of the type locality for *L. ×lacustris*. It is unclear if the range of *L. brevipes* extended further north in the recent past, possibly including Connecticut and Rhode Island, or if these *L. brevipes* × *L. palustris* hybrids achieved their wider distribution as a result of transport by waterfowl or some other means.

Specimens examined. U.S.A. **Connecticut:** New Haven Co., West Pond, Guilford, *Barthlett & Harper s.n.* (NEBC), *Eames 11473* (GH, MSC), *11474* (NEBC), *11474a* (GH), *11475* (GH, PH [type of *Ludwigia ×lacustris* f. *aquatilis*]), *11476* (GH); Lake Clear, North Branford, *Eames & Starr 11192* (MSC); New London Co., Laysville, Old Lyme, *Eames 11494* (GH), *11506* (MSC, NEBC); Rogers Lake, Old Lyme, *Eames 11460* (GH), *11495* (GH), *11496* (GH), *11497* (US), *11503* (NEBC), *Raven 16518* (DS, MO). **Georgia:** Jenkins Co., Jenkins Pond, *Duncan 5645* (GA). **North Carolina:** Cumberland Co., Rhodes Pond, 2 mi. NE of Godwin, *Beal 4481* (NCSC); Harnett Co., Byrd's Mill Pond, S of Bunn Level, with *L. palustris*, *Duke 54–148* (NCU); Johnston Co., 0.5 mi. N of Hardy, *Radford 27952* (FLAS, NCU, SMU), *Ornduff 6461–2* (UC; cult. as *Raven 18106*, MO); Robeson Co., 3 mi. SSE of Lumberton on U.S. 74, *Beal 3195* (DUKE, NCSC). **Rhode Island:** Washington Co., Charlestown, Watchaug Pond, *Eames 11498* (GH [type of *Ludwigia ×lacustris*]). **Virginia:** Virginia Beach Co., *Sargent 6966* (CAS, SMU [mixed with *L. brevipes*]).

Ludwigia arcuata ($n = 16$) × **L. repens** ($n = 24$)

Natural hybrids of this parentage are common in peninsular Florida, an area of extensive overlap between these two species (Fig. 4). The hybrids are fairly widespread within this range, with at least 12 populations documented from six counties, where they were confused with *L. brevipes* and formed the basis for reports of that species from Florida in the past.

Cytological examination of microsporocytes in *Raven 18069* (Citrus Co.) and *Peng et al. 4331* (Hillsborough Co.) consistently showed 16 bivalents and 8 univalents, which agrees with results in artificial hybrids between *L. arcuata* and *L. repens* (Fig. 16). Vegetative characteristics of these natural hybrids closely resemble those of *L. repens*, which is a very common species in this part of Florida. Pollen stainability in *Raven 18069* is 64%, which is similar to the 54%–60% found in artificial hybrids between *L. arcuata* and *L. repens* (Table 4).

Representative specimens examined. U.S.A. **Florida:** Alachua Co., Gainesville, *West & Hodge s.n.* (FSU?); Citrus Co., 4 mi. E of Inverness, *Godfrey 57172* (FSU, GH, IA, USF); Tsala Apopka Lake, *Godfrey 57286* (FSU, IA, LAF, MSC, NY, PAC, TENN, USF, VDB), *Raven 18069* (DS); Cypress areas off FL 48, E of Floral City, *Lakela 25265* (FSU, USF); DeSoto Co., 2.75 mi. S of FL 70, E of DeSoto–Manatee Co. line, *Shuey 2226* (USF); Hillsborough Co., South Lake, Horizon Park, *Chevalier 10* (USF), *Churchill s.n.* (GH); 2.8 mi. N of FL 582, on FL 581 [with *L. arcuata*] *Peng et al. 4331* (MO); Okeechobee Co., 2 mi. S of Basinger, *Lemaire 7* (FLAS); Polk Co., Tiger Bay, *McFarlin 5079* (CAS, FLAS); near Kicco, *McFarlin 5843* (CAS).

Ludwigia brevipes ($n = 24$) × **L. repens** ($n = 24$)

Duke (1955) described a highly fertile specimen from North Carolina (*Duke 54–243*) as morphologically intermediate between *Ludwigia brevipes* and *L. repens*, although he did not explicitly suggest that it was a hybrid. The plant in question apparently was initially emergent, with small (5–7 × 15–20 mm) obovate-elliptic leaves on the lower stems. Because the upper leaves abruptly enlarge (to 10–20 × 30–40 mm), change to oblanceolate-elliptic, and become well-spaced on the upper stems, it seems that the plant was probably inundated subsequently. Under submerged conditions, leaves of *L. brevipes* tend to become narrower (approaching linear), whereas those of *L. repens* tend to become broader

(usually broadly elliptic-obovate to subrotund). The shape of both submerged and emergent leaves of *Duke 54–243* appears to be intermediate between those of the putative parents. Furthermore, the pedicel length is also intermediate (5 mm long) between those of *L. repens* (0–3 mm) and *L. brevipes* (6–15 mm).

Morphology of this hybrid is comparable to that of the experimental hybrid of this parentage (Fig. 15). *Ludwigia brevipes* and *L. repens*, both hexaploid, are interfertile. Artificial F_1 hybrids exhibited complete chromosome pairing at meiotic metaphase I, high pollen viability (over 90%), and normal fruit set.

Specimen examined. U.S.A. **North Carolina:** Dare Co., 3 mi. S of Duck, *Duke 54–243* (NCU).

Ludwigia palustris ($n = 8$) × **L. repens** ($n = 24$)

Both *Ludwigia palustris* and *L. repens* are wide-ranging species that often occur sympatrically, and are separable mainly by flower and fruit characters. They are the only species in section *Dantia* whose ranges extend significantly outside of the U.S.A.; they co-occur in Mexico and the Caribbean. The hybrid population sampled by *Breedlove & Raven 8314* (Mexico, Chiapas) was very abundant, according to the label data. Since the capsules abort without seed set, the plants may primarily propagate themselves vegetatively. *Ludwigia repens* is not known as far south in Mexico as Chiapas, but *L. palustris* is found in other lakes relatively near the one in which the hybrids occur (*Breedlove & Smith 32091*, DS). In morphology this natural hybrid from Mexico is similar to artificial hybrids between *L. palustris* and *L. repens* (Fig. 9). The number of stamens varies from 4 to 6, with the extra stamens occurring in the position of petals; petals are typically lacking in both natural and artificial hybrids (Fig. 9). The plant's cytology revealed 8 bivalents and 16 univalents in meiotic metaphase I, a figure in agreement with that of the artificial hybrid.

A collection from Dare Co., North Carolina (*Duke 54–1*), represents a mixture of two fruiting fragments of *Ludwigia palustris* and seven branches of *L. palustris* × *L. repens* hybrids. Vestigial petals are seen in some flowers and lacking in others in this hybrid collection.

This hybrid combination generally has more or less ovate-elliptic leaves, narrowly obovoid to elongate-pyramidal subsessile ovaries that taper toward the base, ovaries that fail to develop into fruits, petals lacking or vestigial (1 to 4), low level of viable pollen (usually less than 10%), and pollen shed singly. We suspect that such natural hybrids may be more abundant than we have documented, because they often grow vigorously but are not easily recognizable as hybrids. For example, such apetalous hybrids may be misinterpreted as *L. repens*, a species that sheds its petals soon after opening, especially if the pollen viability is not examined.

Representative specimens examined. MEXICO. **Chiapas:** Chéncultik NE of La Trinitaria near Monte Bello Nat. Park, *Breedlove & Smith 32091* (DS); Rancho Nuevo, munic. San Cristobal las Casas, *Breedlove & Raven 8314* (DS). U.S.A. **Florida:** Jackson Co., Lake Seminole, Wildlife Refuge Area, *Monoson 21* (FSU). **North Carolina:** Dare Co., Cape Hatteras Lighthouse, *Duke 54-1* (NCU). GREAT BAHAMA. Eight Mile Rocks, *Britton & Millspaugh 2559* (NY).

Ludwigia palustris ($n = 8$) × **L. spathulata** ($n = 16$)

These hybrids closely resemble *L. spathulata* in leaf shape, flower size, and general appearance. Characters suggesting hybridity include intermediate pubescence, ovaries that turn yellowish pink and abort after anthesis, and a total lack of mature capsules; capsules are usually well-formed a few days after anthesis in both putative parents. There is virtually no viable pollen in this triploid hybrid. *Godfrey 76026* (Florida, Jackson Co.) represents a mixed collection of the hybrid and *Ludwigia spathulata*.

Representative specimens examined. U.S.A. **Florida:** Jackson Co., 3 mi. W of FL 271, N of Sneads, *Godfrey 76026* (MO); Brazzell Lake, *Godfrey 77097* (MO).

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REVISION OF *ANCISTROCLADUS* WALL. (ANCISTROCLADACEAE)[1]

Charlotte M. Taylor,[2] Roy E. Gereau,[2] and Gretchen M. Walters[3]

Abstract

The genus *Ancistrocladus* Wall. ranges from Africa to southeastern Asia and comprises 16 species found in evergreen tropical forests. Unusual morphological features include its dimorphic juvenile and adult habits; an adult sympodial liana habit, climbing by hooks formed from modified stem apices; epidermal pits each containing a single trichome that secretes wax; glands of various forms found on both vegetative and reproductive structures; variously convolute or imbricate corolla aestivation; nutlike fruits with enlarged accrescent sepals; and deeply ruminate seeds. This is the only genus of the Ancistrocladaceae; the family is currently classified in Caryophyllales together with the closely related Dioncophyllaceae. Eleven species are found in Africa, and five in Asia. No infrageneric classification is recognized here. *Ancistrocladus abbreviatus* Airy Shaw subsp. *lateralis* Gereau of Nigeria is newly described herein based on its pedunculate inflorescences that are borne well below the stem apex and its geographic distribution that is disjunct from *A. abbreviatus* subsp. *abbreviatus*. The occurrence of four sepals and petals in the family is reported here for the first time, in *A. grandiflorus* Cheek, as are an additional type of gland found on the leaves, continuous variation from convolute to imbricate corolla aestivation, and the possible occurrence of stipules. Lectotypes are newly designated for *Ancistrocladus stelligerus* Wall. ex DC. and *Bigamea thwaitesii* Tiegh., and a neotype is designated for *A. hainanensis* Hayata. *Ancistrocladus pachyrrhachis* Airy Shaw is reduced to taxonomic synonymy under *A. barteri* Scott-Elliot; *A. uncinatus* Hutch. & Dalziel is reduced to taxonomic synonymy under *A. guineensis* Oliv.; and *A. carallioides* Craib, *A. cochinchinensis* Gagnep., and *A. harmandii* Gagnep. are reduced to taxonomic synonymy under *A. tectorius* (Lour.) Merr.

Key words: Africa, Ancistrocladaceae, *Ancistrocladus*, Asia.

The paleotropical genus *Ancistrocladus* Wall. (nom. cons.; Ancistrocladaceae Planch. ex Walp.) comprises 16 species of lianas found in evergreen tropical forests across Africa and in central through southeastern Asia. *Ancistrocladus* is the only genus in its family, which has only been reviewed previously at the generic level (Gilg, 1895, 1925; Porembski, 2002), though floristic treatments and summaries have been published in the last century for a number of regions in Asia (Steenis, 1948; Ramamoorthy, 1976; Harriman, 1987; Das, 1993; Dagar & Singh, 1999) and Africa (Hutchinson & Dalziel, 1927; Keay, 1954; Léonard 1982, 1986; Lebrun & Stork, 1991; Cheek, 2000).

Ancistrocladus is notable for its unusual habit: it originates as a monopodial, self-supporting sapling, and then becomes a sympodial liana climbing by means of recurved to spiraling, woody hooks formed from the true stem apex (Fig. 1A), with the stem growth then continuing from a subapical meristem. *Ancistrocladus* is also notable for its minute epidermal pits or cone-like depressions that each contain one trichome, which secretes a waxy exudate that frequently then fills its pit; these are found on both surfaces of the leaves and also frequently on the sepals. Additionally the leaves and sepals of *Ancistrocladus* bear glands of several other forms, in particular tiny glands (0.1–0.4 mm diam.) located at the apex of the leaf midrib; large flat glands (large pits of descriptions below, up to 1.0 mm diam., or oblong and up to 4.0 × 1.0 mm in *A. letestui* Pellegr.) scattered on the leaves of many individuals of all species (Fig. 1B); and large (up to 1 mm diam.) rounded or depressed abaxial glands on the bracts of most species and on the sepals of several species (Fig. 1C). Whether these larger glands secrete nectar, wax, or some other substance is unknown. The fruits and seeds of *Ancistrocladus* are also notable: the dry indehiscent nuts are formed from the ovary, receptacle, and ac-

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[2] Research Division, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A. charlotte.taylor@mobot.org; roy.gereau@mobot.org.

[3] William L. Brown Center for Plant Genetic Resources, Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A. gretchen.walters@mobot.org.

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crescent enlarged sepals, which vary from papery to quite hard (Fig. 1G–I), and the solitary, relatively large seeds are deeply ruminate.

Ancistrocladus is further characterized by simple, entire, alternate, spiraled leaves that are apparently estipulate; dichotomously branched, bracteate, pedunculate inflorescences; 4 to 5 imbricate sepals; 4 to 5 white or yellow to red petals that are usually very shortly coherent or connate at their bases and variously convolute or imbricate in bud; 5 to 15 stamens with filaments that are shortly connate and/or notably thickened at their bases, dithecal anthers that open by longitudinal slits, and a connective that is sometimes enlarged relative to the thecae; a partially to fully inferior, unilocular ovary that has a single basal ovule and usually an apical disk; and three stigmas borne on a single united style or on three separate styles. The occurrence of 4 sepals, petals, and stamens is reported for this family here for the first time; this condition is found only in *A. grandiflorus* Cheek. The occurrence of the various types of larger pits and their taxonomic and morphological distribution are also reported here for the first time.

The presumed relationships and classification of *Ancistrocladus* have varied widely. Tieghem (1903) and Léonard (1949) have summarized its various taxonomic placements during the 19th century and the first part of the 20th century, which include Malpighiaceae, Combretaceae, Symplocaceae, Myristicaceae, Annonaceae, Dipterocarpaceae, and in its own family, Ancistrocladaceae. In the 20th century Gilg (1925) placed the Ancistrocladaceae in the Parietales, and Cronquist (1981) placed it in the similarly constituted order Violales, together with the closely related family Dioncophyllaceae. Dioncophyllaceae comprise three African genera of lianas, which are closely related to Ancistrocladaceae (Cameron et al., 1995). These two families share anatomical (Metcalfe, 1952; Gottwald & Parameswaran, 1968), pollen (Erdtman, 1958), and chemical (Bringmann et al., 1990) characters; Dioncophyllaceae are separated from Ancistrocladaceae by a superior ovary, numerous parietal ovules, capsular fruits, and their habit with the plants climbing by hooked leaf tips. Most recently, Porembski (2002) and Stevens (2004) have classified the Ancistrocladaceae in the non-betalain Caryophyllales based primarily on molecular systematic studies.

Ancistrocladus can be confused with several lianas that climb by similar-appearing hooks of various developmental origins, though none of these bear the small pits on their leaves that are characteristic of *Ancistrocladus*. *Artabotrys* R. Br. ex Ker Gawl. (Annonaceae) has hooks formed from modified peduncles rather than modified stem apices and can be separated vegetatively from *Ancistrocladus* by its aromatic tissues and distichous leaf arrangement. *Uncaria* Schreb. (Rubiaceae) also has hooks formed from modified peduncles, and can be separated from *Ancistrocladus* by its opposite leaves, paired hooks, and large, usually persistent interpetiolar stipules. Dioncophyllaceae can be separated by the position of the hooks, at the leaf apices rather than along the stems. *Hugonia* L. (Linaceae) has hooks formed from modified lateral stems, and can be separated from *Ancistrocladus* by its dentate leaves and usually paired hooks. *Anacolosa* (Blume) Blume (Olacaceae) has hooks formed from modified petioles and can be separated from *Ancistrocladus* by its distichous rather than spiral leaf arrangement. Hallé (1973) additionally distinguished several genera of lianas in central Africa, including *Ancistrocladus*, by the degree of curvature of their hooks.

Ancistrocladus is found in wet to seasonal, lowland to submontane (e.g., *A. letestui*, *A. tanzaniensis* Cheek & Frim.), evergreen forests in Africa (11 species) from Senegal to Kenya and Tanzania (Fresson, 1967), and also in dry to wet, lowland to submontane (*A. tectorius* (Lour.) Merr.), evergreen Asian forests (5 species) from India and Sri Lanka through Myanmar, Thailand, Cambodia, Laos, Vietnam, China (Hainan Island), Malaysia, Singapore, the Andaman Islands, and Sumatra (Steenis, 1948; Stevens, 2004). It is distributed in the Guineo-Congolian, Sudano-Zambezian, Indian, Indochinese, and Malesian Regions of Takhtajan (1986), and the Africa and Asia/Tropical areas of Hollis and Brummit (1992).

Ancistrocladus is found in primary forests, secondary forests, swamps, seasonally inundated riverside forests, along roadsides, and in cultivated and other disturbed areas. Specimen data from Africa report that the plants are frequently collected along streams and rivers; very little information about microhabitat is available from Asian collections. *Ancistrocladus* appears to be quite abundant on several islands, in particular the Andaman Islands (Dagar & Singh, 1999) and Sri Lanka (Thwaites, 1849), and there to reproduce widely through vegetative means. However, Foster and Sork (1997) found local population densities to be quite low in *A. korupensis* D. W. Thomas & Gereau in a mainland forest in Cameroon, where that species does not reproduce vegetatively and shows low seedling recruitment. Foster and Sork (1997) also found *A. korupensis* populations to be highly inbred with low allozyme diversity and apparently very limited seed

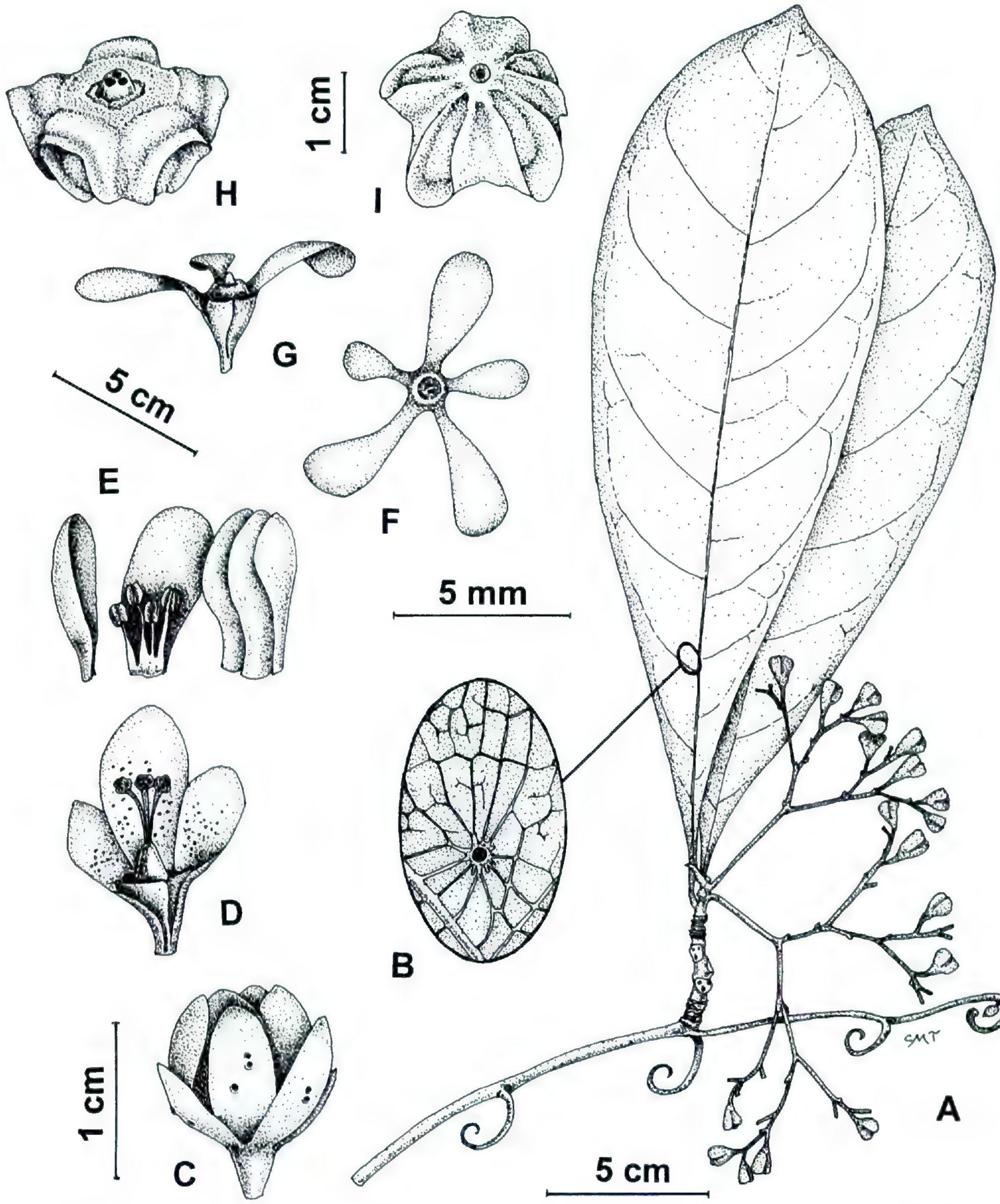

Figure 1. A–E. *Ancistrocladus grandiflorus* Cheek; based on *Gereau et al. 5594* (MO). —A. Portion of flowering branch, with inflorescence bearing old flowers from which petals have fallen and on which sepals have started to enlarge (the most commonly collected fertile stage of most *Ancistrocladus* species). —B. Detail of abaxial leaf surface of Figure 1A, showing portion of secondary vein on lower left and a "large pit." —C. Flower at anthesis. —D. Partially dissected flower showing ovary portion, styles, stigmas, and three sepals. —E. Partially dissected flower, showing petals and 4 (of 10) stamens. F, G. Fruit of *Ancistrocladus korupensis* D. W. Thomas & Gereau; based on Thomas and Gereau (1993: fig. 1C, D). —F. Apical view. —G. Side view. H, I. Fruit of *Ancistrocladus likoko* J. Léonard; based on *Ghesquière 2780* (BR). —H. Oblique apical view. —I. Basal view. A to lower 5-cm scale; B to 5-mm scale; C, D, E to same 1-cm scale; F, G to same 5-cm scale; H, I to same 1-cm scale.

dispersal. Most species of *Ancistrocladus* are known from relatively few collections, perhaps because they flower infrequently and because the flowers and fruit are often inaccessible, being borne high in the forest canopy. *Ancistrocladus* is frequently collected while sterile, no doubt because the plants are vegetatively unusual and distinctive; however, identification of sterile specimens below the level of genus is difficult at best.

Ancistrocladus produces a number of alkaloid secondary compounds that have been of interest both phytochemically and pharmacologically. Its

naphtylisoquinoline alkaloids are otherwise found only in Dioncophyllaceae (Bringmann et al., 1990; Bringmann & Pokorny, 1995; additional references cited in Lebrun & Stork, 1991). Some of these alkaloids have shown significant activity against malaria (François et al., 1994) and one group of these, the michellamines produced by *A. korupensis*, were found to have significant inhibitory activity against the human immunodeficiency virus (HIV) (Manfredi et al., 1991; Boyd et al., 1994; Foster & Sork, 1997). However, in preclinical studies in several animal models, michellamine B was found to possess significant neurotoxicity, which precluded it being advanced into clinical trials (pers. comm., Gordon Cragg, Natural Products Branch, Developmental Therapeutics Program, National Cancer Institute, U.S.A.).

History

Wallich (1829) named *Ancistrocladus* in his catalogue of Indian and Southeast Asian plants. Here he listed four species from India, Sri Lanka, Burma, Malaysia, and the Andaman Islands. *Ancistrocladus* had been previously named by two other authors, however; Loureiro (1790) published *Bembix* Lour., based on *B. tectoria* Lour. from what is today Vietnam, and Vahl (1810) published *Wormia* Vahl, based on *Wormia hamata* Vahl from Sri Lanka. Vahl's name, however, is a later homonym of *Wormia* Rottb., published (Rottbøl, 1783) for a genus of plants now treated in the Dilleniaceae and thus is illegitimate and cannot be used. *Bembix* was validly published, but Wallich's name was conserved over it and the Sri Lankan species was chosen as its conserved type, as listed in ICBN Appendix IIIA.E3 (Greuter et al., 2000: 265). Subsequently, Endlicher (1840) published *Bigamea* K. Koenig ex Endl. for the Sri Lankan species. Neither Koenig nor Endlicher named any species of *Bigamea*, although they clearly considered there to be only one species of this genus in Sri Lanka.

Although Planchon (1849) first recognized the Ancistrocladaceae as a separate family, then comprising one genus with seven species from India, Sri Lanka, and southeastern Asia, Walpers (1851) first validly published this family name. This family was not recognized for several subsequent decades by most authors, who classified *Ancistrocladus* in a variety of other families but most often in the Dipterocarpaceae, largely because of its similar fruits. However, the family Ancistrocladaceae was generally recognized by the end of the 19th and beginning of the 20th century (Gilg, 1895, 1925; Tieghem, 1903).

Oliver (1868) first reported *Ancistrocladus* from Africa when he described *A. guineensis* Oliv. as a species of Dipterocarpaceae from Nigeria. Subsequently, *Ancistrocladus* was reported from central Africa (Léonard, 1949, 1982) and later documented in west Africa (Airy Shaw, 1949, 1950) and in east Africa (Freson, 1967; Léonard, 1984, 1986; Cheek et al., 2000).

Tieghem (1903) reviewed Ancistrocladaceae with particular emphasis on its anatomy and recognized three genera in the family: *Bigamea*, distinguished by having only five stamens and comprising the *Ancistrocladus* plants found in Sri Lanka, which he treated as two species; *Ancistrella* Tiegh., distinguished primarily by anatomical details and comprising one African species, *Ancistrella barteri* Tiegh.; and *Ancistrocladus*, comprising the remaining species including the one other African species known to Tieghem, *Ancistrocladus guineensis*. Tieghem knew *Ancistrella barteri* only from one sterile collection, but considered it distinct from *Ancistrocladus* due to its larger and apically more acute leaves, its different arrangement of fiber bundles in the leaf midrib, and its distinctive stem epidermal structure, composed of parallel-elongate cells that lack chlorophyll and have thick but non-lignified walls.

Gilg (1895, 1925), however, treated all these species in one genus, though in his second review of the family (Gilg, 1925) he separated the Sri Lankan plants in *Ancistrocladus* sect. *Bigamea* (K. Koenig ex Endl.) Gilg, which comprised only the section's type species, *A. hamatus* (Vahl) Gilg. All the remaining species he placed in "Sect. *Euancistrocladus*," which is correctly called *Ancistrocladus* sect. *Ancistrocladus* under our current rules of nomenclature (Greuter et al., 2000). Subsequent authors have agreed in placing all of the species of Ancistrocladaceae in only one genus, *Ancistrocladus* (Cronquist, 1981; Porembski, 2002; Stevens, 2004).

Morphology

Habit

Ancistrocladus species are usually found as lianas climbing high into the forest canopy by means of their distinctive lateral branches that bear several woody hooks. However, they begin life as erect, self-supporting saplings in their juvenile stage, and the climbing growth develops later from extra-axillary stems (REG, pers. obs., *A. grandiflorus*, *A. korupensis*, *A. letestui*, Africa), which may at times appear to be terminal (CMT, pers. obs., *A. robertsoniorum* J. Léonard, MO greenhouse). These

climbing stems comprise elongated main stems that bear vegetative, often robust leaves that are usually well spaced along these stems, and smaller lateral branches that are sparingly branched and bear the distinctive hooks as well as clusters of leaves and inflorescences. In most, if not all, *Ancistrocladus* species, the leaves of these different stems are markedly different in size and sometimes in shape. Usually the leaves of the saplings are relatively large and narrowly oblanceolate, the leaves of the ultimate stems are ¼–½ as large and generally elliptic to obovate or oblong, and the leaves of the main climbing stems are usually intermediate between these in both size and shape. A number of collections (including type collections, e.g., that of *A. hamatus*) comprise two or more types of stems and leaves, and unknowing comparisons among different growth stages have created some confusion in the delimitation of *Ancistrocladus* species and their identification.

The growth of the climbing stems of *Ancistrocladus* is developmentally complex (Fig. 1A), as noted by a number of authors and described in some detail by Gilg (1925), Tieghem (1903), Hallé (1973), and notably Massert (1896). In his general study of heteroclady in tropical lianas, Massert studied living plants of several species of *Ancistrocladus* growing in a common garden in Java through both observation and experimental manipulation. He reported consistent differences in growth pattern among some of the species; this has not subsequently been investigated in the field but may be informative with respect to the systematics of this group. He described the growth of the lianescent stems as fundamentally sympodial from buds borne singly, paired, or in groups of three in the axils of some leaves, while other leaves lack axillary buds. He found the buds at a particular position to be generally determinate in whether they would produce a stem with well-developed internodes, a leafy lateral branch, or a hook. He also reported that damage to the lianescent stems resulted in further sympodial growth, with no return to the monopodial, presumably juvenile mode of growth. Thwaites (1849), however, reported plants of *A. hamatus* of Sri Lanka to have extensive vegetative reproduction from rootstocks or rhizomes at least in disturbed secondary sites. Massert (1896: 134–135, figure reproduced by Gilg, 1925) described in detail the growth pattern found in *A. vahlii* Arn. [= *A. hamatus*] and *A. pinangianus* Wall. ex Planch. [= *A. tectorius*], which he said had the most complex growth patterns of the species that he observed. His description of this growth pattern of these species was then summarized by Gilg (1925), who to some extent implied it to be the characteristic growth pattern of the family by only describing this one pattern.

As described carefully by Massert (1896), Tieghem (1903), and Hallé (1973), the lianescent growth of *Ancistrocladus* is basically sympodial, in the elongated stems with regularly spaced leaves and in the leafy, hook-bearing lateral branchlets. These authors all regarded the growth as composed of sympodial units that develop in a characteristic way. This sympodial unit begins as part of the elongated stem, where it develops several monopodial internodes and then an internode in which the growth form changes, with the elongated stem continued sympodially from a lateral bud and the last monopodial segment of the sympodial unit becoming a lateral extension that terminates in a hook. Growth as a lateral branchlet then continues, developing from buds borne below the hook and in some cases with the subsequent stem apex or apices also becoming hooks and the branchlet growth again continuing from subapical buds. These hooks are initially sensitive, wrapping around other structures as available to support the liana's stems, and later become woody. The lateral branchlets usually produce one to several hooks, which are sometimes associated with reduced, persistent or caducous leaves that are borne below the hook or occasionally on it; distally to the hooks these branchlets then produce a group of leaves. The leaves borne along these lateral branchlets vary from well-spaced along it to laxly to densely clustered at its end. These lateral branchlets may also bear additional branchlets and/or inflorescences, both arising from extra-axillary positions. Hallé (1973) studied different species than Massert and Tieghem, and his interpretation of the individual sympodial units that comprise the lateral branchlets differs in some details from theirs. Keng (1970: 235) provided a markedly different interpretation from all other authors: he discovered occasional plants of *Ancistrocladus tectorius* in which the hooks terminated in a reduced sterile flower during the flowering season (cf. flowers borne singly on hook-bearing branches from sapling in *A. korupensis, Gereau & Thomas 5204*, MO), as well as an unusual plant in which "the cirrhate branches are much excessively ramified, comparable closely to a fully developed inflorescence," and concluded that the sympodial branching of *Ancistrocladus* "represents the modified peduncles and pedicels of a partially developed inflorescence," similar to the hooks of *Artabotrys*.

Tieghem (1903) described the anatomy of several species of *Ancistrocladus*, and his work was later

summarized by Metcalfe (1952). Some additional anatomical aspects were investigated by Gottwald and Parameswaran (1968) and Keng (1967), and further discussed by Porembski (2002). Although Tieghem considered the anatomical characters of the half-dozen species he studied to be informative at the species and genus level, subsequent authors have not confirmed or adopted his views, nor do we in the present work.

INDUMENT AND GLANDS

All plants of *Ancistrocladus* examined lack external indument and have been characterized as glabrous by previous authors (Tieghem, 1903; Metcalfe, 1952), but all bear characteristic small pits ("petites cryptes," Tieghem, 1903: 159; "peltate glands," Metcalfe, 1952: 366; Metcalfe & Chalk, 1972: 221) as well as one or more types of glands or larger pits that have not previously been described in detail. Also not previously noted are the characteristic epidermal structures found in one African species: many (though not all) plants of *A. letestui* can be recognized by the tiny (0.2–0.3 mm long) protuberances of the epidermis found on young branches, and which sometimes persist on older branches. These protuberances are stout, multicellular structures that resemble the branchlet bark in color and texture and are continuous with it, and are here interpreted as epidermal ornamentations rather than trichomes. Nothing is known of the structure and function of these protuberances. The tissues of *Ancistrocladus* are not aromatic and do not have any other notable odor (REG, pers. obs., Africa; CMT, pers. obs., MO greenhouse).

Tieghem (1903: 159) was the first and apparently only person to study the small pits in any detail, despite their earlier mention by Planchon (1849) in the diagnoses of several species and by Candolle (1868) in his treatment of the family. Tieghem noted that these numerous small pits ("petites cryptes") are inverted cone-like depressions of the epidermis, each containing a single trichome. In living leaves, the small pits and the tops of their included trichomes are typically visible with a hand lens; however, on some dried specimens these may be difficult to see even with good magnification. These small pits are generally 0.1–0.2 mm in diameter. The trichome in the pit exudes a white waxy substance that often fills its depression and sometimes bulges upward, giving the leaf noticeable dots seen even with the naked eye; these dots may appear white or black, perhaps depending on the nature or age of the exudate. The amount and color of the exudate produced varies among the pits even on a single leaf, although the pits of a given part of the leaf appear to be generally similar in this production. This exudate has long been described as "waxy," based on Tieghem (1903), but apparently has not been studied in detail. These small pits are found on both surfaces of both juvenile and adult leaves, where they are usually located in the areoles between the higher-order veins but occasionally on the tertiary veins themselves, and on either or both surfaces of the sepals (Fig. 1D) of some species. In several *Ancistrocladus* species the small pits are regularly and densely distributed (i.e., one to three per areole), while in other species they are rather sparsely distributed with their concentration usually highest near the midrib and margins. The function of these small pits is unknown.

No previous mention has been made of the scattered large pits found on the adaxial and sometimes also abaxial surfaces of the adult leaves of *Ancistrocladus* species (Fig. 1B). These large pits or glands are usually 0.1–1.0 mm in diameter (or sometimes larger and oblong in *A. letestui*), and on dried specimens are often black. They appear at least sometimes to produce a waxy substance, but their function is unknown. These large pits lie flat on the leaf surface with no trichomes visible within them. They are located at junctions of several tertiary veins, and usually encircled by a raised ring formed by the union of these veins. At least on dried specimens their location is sometimes evident on the opposite surface by an associated depression or small protuberance. These large pits occur in every species of *Ancistrocladus*, though they are not always present on all leaves of an individual plant. These large pits generally do not distinguish individual species, although in *A. letestui* those located near the petioles are rather elongate while those of all other species are circular to slightly oblong.

Most leaves, both juvenile and adult, of all *Ancistrocladus* species additionally bear tiny glands (0.1–0.4 mm diam.) at their adaxial apices. These glands are usually situated at the end of the midrib, which typically does not extend to the very end of the leaf tissue, but disappears or reticulates 0.5–1.0 mm short of it. The structure of these tiny glands has not been studied, and the type of exudate they produce as well as their function is unknown.

Glands are also found in many *Ancistrocladus* species on the inflorescence bracts and the sepals. The glands of the inflorescence bracts are relatively large (0.5–1.0 mm diam.), shortly raised or depressed (although in this second case at least sometimes they seem to have collapsed in drying), and appear to produce a clear or sometimes white waxy

exudate. They are located on the abaxial (i.e., outer) surface of the bracts, and usually cover half or more of it. A few species lack these glands (e.g., *A. korupensis*), and the presence or absence of these glands appears to be a reliable character for distinguishing some species although the form and presence of these glands seems to vary within several individual species (e.g., *A. tectorius*). Glands similar to these are also found on the abaxial surface of the two or three outermost sepals of some species (Fig. 1C), though these sepal glands are typically surrounded by a raised circular to oval border. Keng sectioned and stained flowers of *A. tectorius* and described these sepal glands: "They are apothecium- or perithecium-like in the sectional views with a large number of segmented hypha-like glandular hairs compactly arranged" (Keng, 1967: 114). The type of exudate produced by these bract and sepal glands is unknown, and their structure apparently has not been studied in any further detail.

LEAVES

The leaves are simple, alternate, and spirally arranged, although they are sometimes so densely grouped at the apices of the sapling stems and the lateral branchlets of the lianas that their arrangement is difficult to discern (Fig. 1A). In bud the leaves are tightly rolled longitudinally. The leaves are sessile to subsessile, though they sometimes appear to be petiolate due to the blade tissue that extends to the petiole base being markedly narrowed. This condition has been called "pseudopetiolate" (Léonard, 1949, 1986). All the leaves of *Ancistrocladus* seen are entire, though Gilg (1925) reported that they may occasionally be crenate but without naming a species or source for this observation. The leaves vary from elliptic or obovate to very narrowly oblanceolate. Several species include specimens that have very narrow leaves, but there is variation within these species (e.g., see the discussion under *Ancistrocladus letestui*) so this feature does not appear to be a reliable character to distinguish individual species, although the ratio of leaf length to width (L/W) is of some taxonomic utility. The leaves vary markedly in size both in the genus and within individual species; similarly this character does not appear to be consistent within species or useful to distinguish individual taxa (e.g., see the discussion of *A. pachyrrhachis* Airy Shaw under *A. barteri* Scott-Elliot). The leaves appear to be long-lived, apparently persisting a year or more on the plants.

The leaves are variously said to be exstipulate (Tieghem, 1903; Stevens, 2004) or stipulate with tiny, quickly caducous stipules (Léonard, 1949; Cronquist, 1981; Porembski, 2002). Gilg (1925) contributed to the confusion here by reporting both conditions: in his formal morphological description of Ancistrocladaceae he reported small caducous stipules, but in his discussion of leaf morphology in the same article he reported that stipules are lacking. Neither stipules nor stipule scars are evident on herbarium specimens, but small (up to 1 mm long), fugaceous, triangular structures located on either side of the base of the leaf blade are found on living plants when the leaves flush, and sometimes leave scars after falling (CMT, pers. obs., *Ancistrocladus robertsoniorum*, MO greenhouse). The origin of these structures has not been investigated anatomically, but they are here provisionally considered to be stipules. The presence of these structures on all species of *Ancistrocladus* has not been confirmed.

The leaf midrib is notably well developed and usually markedly thickened at the base. When the leaf falls, this thick midrib leaves a relatively large (i.e., 2.0–4.5 mm wide) leaf scar. The leaf venation is brochidodromous to eucamptodromous. The secondary and tertiary veins are well developed and extensively reticulated, so that the secondary veins are sometimes difficult to distinguish from the higher-order venation. This vein reticulum is usually raised on one or both surfaces of the leaf. The leaves also bear epicuticular wax platelets that are similar to those of Dioncophyllaceae (Ditsch & Barthlott, 1994).

INFLORESCENCES

The inflorescences are borne on the lateral branchlets, usually several per branchlet, from extra-axillary positions below the apex (Fig. 1A) except in *Ancistrocladus abbreviatus* Airy Shaw subsp. *abbreviatus*, where the inflorescences are typically solitary and produced so close to the branchlet apex that they appear terminal. Subterminal or apparently terminal inflorescences sometimes occur in *A. guineensis*, *A. heyneanus* Wall. ex J. Graham, and *A. letestui*. The inflorescences are several- to many-flowered, indeterminate, bracteate, and usually pedunculate. They are generally branched dichotomously to several orders, or in several species the basal portion of the inflorescence is regularly dichotomous but the distal portions are racemiform and often quite prolonged (e.g., *A. barteri*, *A. heyneanus*). The flowers are borne separately along the axes and are usually pedicellate with the pedicels often thickened, except they are sometimes sessile in some plants of *A. heyneanus*. Pedicel measure-

ments in the descriptions below are made from the point of the pedicel's separation from the inflorescence axis to the point of its articulation below the flower. This articulation point is probably the base of the inferior ovary, but that is difficult to determine because the ovary tapers to its base, the pedicels themselves are usually thickened distally, and the sepals are usually unequally decurrent along the ovary. The flowers are usually subtended by one to several bracts, which may be caducous. Occasionally some bracts near the base of the inflorescence are leaflike, or are replaced by small leaves; these structures are here called bracteal leaves.

FLOWERS

The flowers of *Ancistrocladus* are bisexual and actinomorphic with a partially to fully inferior ovary and a well-developed disk and are generally 5–12 mm wide (Fig. 1C). No information appears to be available on floral visitors or pollinators. Based on their size and general morphology, the flowers are presumably visited by small insects; with one exception, no odor has been reported by collectors for the flowers, and the nature of any floral reward is unknown. The only floral biology reported for any species in this genus is the label data for *D. W. Thomas 9971* (MO), which describe flowers of *A. korupensis* in Cameroon as opening at night and having a faint aromatic odor.

There are five or rarely four (*Ancistrocladus grandiflorus*) oblong to obovate sepals that vary from generally equal in size (e.g., *A. ealaensis* J. Léonard) to markedly unequal (e.g., *A. korupensis*). The sepals are imbricate in bud with their bases usually at least shortly decurrent on the ovary (Fig. 1D). As noted above, the sepals frequently bear the same small pits found on the leaves, and often the two or three outermost sepals have well-developed abaxial glands borne medially.

The obovate to elliptic petals are also five or rarely four (*Ancistrocladus grandiflorus*), and are equal in size and shape. They are usually somewhat thickened at the base and concave or cucullate toward the apex (Fig. 1E). The petals at least sometimes are shortly connate at their bases, and vary from pale green, white, yellow, or orange to red, with some color variation reported by collectors for most species. At anthesis the petals seem to remain generally erect while the sepals usually spread widely. There is little variation in shape of these structures among species of *Ancistrocladus*; there is a little variation in size among some species. In bud the petals may be convolute, imbricate, or intermediate in arrangement. Their arrangement appears to be consistent within several species (e.g., *A. korupensis*), but to vary in a few species from convolute to intermediate (e.g., *A. barteri*, *Leeuwenberg 2709*) or continually from convolute through intermediate to imbricate (e.g., *A. congolensis* J. Léonard, *Léonard 1513*, *Germain 5049*). We here describe corolla aestivation as convolute (Lawrence, 1951: 746; "contorted" of Stearn, 1992: 333) when each petal has one lateral margin exposed in bud, and as imbricate when one petal has both lateral margins exposed (i.e., the petal is "external") and when one petal has both lateral margins covered (i.e., the petal is "internal"). Corolla aestivation is here considered intermediate when one petal has both lateral margins exposed (i.e., the petal is "external"), and when the "external" petal is removed each of the four remaining petals has one lateral margin exposed and one covered with respect to each other, so that none of the petals has both lateral margins covered and none can be considered "internal." Neither this intermediate condition nor the variation in corolla aestivation within a species has been noted by previous authors.

The stamens are generally 10 arranged in one or two whorls, except in *Ancistrocladus grandiflorus* they are sometimes only eight and in *A. hamatus* they are reduced to five and are alternate to the petals. The filaments are shortly fused at their rather thickened bases and are adnate to the bases of the petals. Filament length is generally correlated with petal size, so that the anthers are positioned at or below the middle of the petals. In some species (e.g., *A. congolensis*) the filaments are generally equal in length but in several species they are dimorphic in length, with the filaments of the outer whorl opposite to the petals and shorter than the filaments of the internal whorl, which are alternate to the petals (e.g., *A. korupensis*; Fig. 1E). Léonard (1986) reported as many as 15 stamens for *A. robertsoniorum*, but we have not observed more than 10 stamens in this species. Ramamoorthy (1976) described *A. heyneanus* in southwestern India as having 9 stamens with 4 of them reduced to staminodes, apparently based on study of a single flower. We have not seen this flower; however, his description of the genus in this same work makes no mention of any size dimorphism among the stamens of *Ancistrocladus*, though this is a notable feature of the genus that is rarely overlooked. Thus it seems possible that Ramamoorthy misinterpreted the stamens of the shorter outer whorl as staminodes. The anthers comprise two thecae usually separated by a well-developed connective and are dehiscent by introrse longitudinal slits. In most species the anthers of an individual flower seem to be generally

similar in size, even when the filaments are dimorphic. Keng (1967) found some flowers of *A. tectorius* had anthers of the same size regardless of filament length, while other flowers of the same species had anthers that were dimorphic in size with the longer filaments bearing larger anthers. The pollen is 3-colpate and oblate to suboblate with a spinulose tectum (Erdtman, 1958; Porembski, 2002: fig. 6).

The ovary is 3-carpellate but unilocular with a single basilateral ovule. The ovary has been variously considered to be inferior or semi-inferior, based at least in part on differing interpretations of structures at the center of the flower (Tieghem, 1903). The ovary is crowned in the flower by a disk and a short columnar structure; these both persist in fruit and have sometimes been interpreted as part of the ovary, but other times as a separate structure (Tieghem, 1903). Tieghem (1903) considered the ovary fully inferior, but it does appear to be only partially inferior in the flowers of several species (e.g., *A. grandiflorus*, *A. guineensis*, *A. letestui*). The persistent basal stylar column bears three or infrequently one (*A. ealaensis*, *A. likoko* J. Léonard) deciduous styles and three capitate to depressed-globose stigmas. The number of styles has been considered taxonomically informative by Léonard (1949), and is considered informative here. The ovule is hemianatropous and bitegmic.

FRUITS AND SEEDS

The accessory fruit of *Ancistrocladus* is an indehiscent nut formed by the ovary, the persistent disk and style base, and the five accrescent sepals that enlarge markedly during fruit development to form obovate to spathulate wings 5–50 mm long (Fig. 1G–I). The "nut" or ovary portion is generally turbinate in shape with the pericarp rather leathery to stiff. There is some taxonomically useful variation in the size (but not the shape) of the nut portion among different species, as well as some differences in ornamentation of its sides. These ornamentations usually comprise ridges or flanges that arise from the decurrent sepal margins, and which seem to be distinctive for some species (e.g., *A. likoko*, Fig. 1H, I). The form of the fruit wings also varies among species, in particular the size of the wings and whether they are equal or not, spathulate or obovate, and papery or stiff.

The fruits of *Ancistrocladus* have been compared to those of Dipterocarpaceae and assumed to be adapted for wind dispersal. Many collectors of *Ancistrocladus* report that the plants often grow along roads, rivers, and streams, edge habitats that provide opportunities for wind dispersal. However, a few species (e.g., *A. ealaensis*, *A. likoko*) inhabit swamp forests and have fruits with smaller wings and heavier "nuts" that superficially resemble those of *Trapa* L. (Trapaceae); the fruit wings of these species and perhaps other species may serve at least in part to orient the fruits while they are floating in water. In the nearly windless forest habitat of Korup National Park, Cameroon, the elongated, papery wings of the fruits of *A. korupensis* apparently serve to orient the "nut" in an upright position on the forest floor to prevent dessication of the radicle after germination (REG, pers. obs.).

The seeds of *Ancistrocladus* are solitary, oblate to subglobose, relatively large (5–8 mm diam.), and distinctive in their deeply ruminate endosperm that is covered with a smooth, thin-textured, reddish brown testa. The endosperm is starchy and the embryo straight. Tieghem (1903) described the ovule, seed, and embryo morphology in some detail.

TAXONOMIC TREATMENT

The treatment here is based on study of herbarium specimens from A, ANSP, BM, BR, C, E, EA, FHI, GC, GH, HAKS, IBSC, KYO, L, MO, P, PNH, SING, TI, US, and WAG, and some field observations (REG) in central and eastern Africa. Flowers, when available, were measured in their dried condition or sometimes revived using water or Pohl's softening solution (Pohl, 1965); this rehydration did not appear to affect the absolute or relative sizes of floral parts. In keys and descriptions "L/W" indicates the ratio of length to width of a given organ, which is expressed here by only the larger number with its comparison to 1 implied. For example, the ratio "4.2:1" is here written as "L/W 4.2." In descriptions, information presented in parentheses describes a rare condition or a clarification, while information presented in brackets has not been confirmed by us.

We first present a key to all the species of *Ancistrocladus*, with flowering and fruiting material keyed separately to facilitate identification because flowers and fruits of *Ancistrocladus* species are rarely collected together. The flowers or fruits of a few species are still unknown; these exceptions are noted at the appropriate places in the key. It is not possible to separate all species of *Ancistrocladus* based only on fruit characters, but they can all be distinguished by their flowers. Separate keys to the species of Africa and Asia, respectively, for more rapid identification are presented in Appendix I.

Selected vouchers for geographic distribution and morphological variation are detailed under each species. These specimens are chosen to in-

clude distributional vouchers for each major political division in each country, except in the case of Cambodia (20 provinces), Laos (18 provinces), and Vietnam (58 provinces), where the divisions are numerous and the specimens are instead chosen to indicate general distribution within the country. Country names used here follow the U.S. Central Intelligence Agency's World Factbook, <http://www.cia.gov/cia/publications/factbook/>, consulted August 2004. Appendix II includes a list of all the numbered collections studied with their identifications.

The conservation status proposed here for the African species is provisional. IUCN criteria (IUCN, 2001) are used, and the abbreviation "EO" is used for Extent of Occurrence. The conservation status assessments were prepared by GMW in consultation with regional experts on the varying degrees of threats to the habitats and protected areas in which each species is found. For each African species, we compare our provisional conservation status with that proposed by Cheek (2000) according to the criteria used by IUCN (1994). Conservation status is not assessed here for the Asian species due to our lack of knowledge of forest conservation in that region.

Ancistrocladus Wall., Numer. List. 1052. 1829, nom. conserv. *Wormia* Vahl, Skr. Naturhist.-Selsk. 6: 104. 1810, hom. illeg., non *Wormia* Rottb., 1783 [Dilleniaceae]. TYPE: *Ancistrocladus hamatus* (Vahl) Gilg [ICBN Appendix IIIA, thus protected under Art. 14.8] [basionym: *Wormia hamata* Vahl].

Bembix Lour., Fl. Cochinch. 259, 282. 1790, nom. rejic. TYPE: *Bembix tectoria* Lour. [= *Ancistrocladus tectorius* (Lour.) Merr.].

Bigamea K. Koenig ex Endl., Gen. Pl. 1183. 1840. *Ancistrocladus* sect. *Bigamea* (K. Koenig ex Engl.) Gilg, Nat. Pflanzenfam. ed. 2, 21: 580. 1925. TYPE: *Ancistrocladus hamatus* (Vahl) Gilg (lectotype, selected by Gilg (1925: 580)).

Ancistrella Tiegh., J. Bot. (Morot) 17: 155. 1903. TYPE: *Ancistrella barteri* Tiegh. [= *Ancistrocladus abbreviatus* subsp. *lateralis* Gereau].

Lianas or scandent shrubs climbing by hooked apices of sympodial branches, with juvenile growth often heteromorphic, erect, shrubby, monopodial, unbranched or sparsely branched, and without hooks, with adult growth comprising elongated, usually little-branched stems (i.e., main stems) that bear smaller extra-axillary lateral stems (i.e., branchlets); plants externally glabrous, not succulent, not aromatic, often with calcium oxalate crystals, normally without adventitious roots; branches extra-axillary; hooks extra-axillary, sensitive, recurved to spiraled, becoming woody, generally borne in a single plane along branch. *Leaves* alternate, spiral, simple, entire, sessile though often appearing pseudopetiolate due to long-attenuate base of blade, often long-lived, exstipulate or with stipules small and caducous, on adaxial and abaxial surfaces with sparsely to moderately distributed small pits, with each pit containing (and filled by) a single trichome that secretes a waxy substance, at least sometimes heterophyllous with the juvenile leaves crowded in terminal rosettes, the *adult leaves* variously distributed along stems (i.e., stem leaves) and/or crowded at apices of lateral branchlets or stems (i.e., leaves borne at apices of branchlets), these sometimes clustered in terminal rosettes, often with some glands or large pits located at the junctions of groups of tertiary veins; midrib usually extending to apex and terminating in a tiny gland; secondary veins usually brochidodromous, sometimes only weakly so or eucamptodromous; tertiary venation irregularly and often finely areolate; leaf base articulated at stem, usually leaving a relatively large scar (2.0–4.5 mm wide). *Inflorescences* lateral (i.e., extra-axillary; pseudo-terminal, Léonard, 1949, 1986) or sometimes apparently terminal on lateral branchlets, 1 to several per branchlet, paniculate, congested to usually lax, dichotomously branched or sometimes with higher-order axes becoming racemiform, subsessile to usually pedunculate, sometimes bearing hooks, usually bracteate, the bracts subtending axes and pedicels, often with 1 to several abaxial glands, sometimes the lower bracts replaced by small but clearly developed leaves (bracteal leaves). *Flowers* hermaphrodite, actinomorphic or with the sepals unequal, epigynous to partially hypogenous, pedicellate or rarely sessile (*A. heyneanus*), pedicels articulated at base of ovary; *sepals* 5 or rarely 4 (*A. grandiflorus*), free to shortly fused at base, usually decurrent on ovary, imbricate, equal to unequal with (2)3 sepals larger than and external to 2 smaller sepals, accrescent on fruit, often with small pits on one or both surfaces, sometimes with 1 to several abaxial glands; *petals* 5 or rarely 4 (*A. grandiflorus*), free to shortly fused at base, in bud imbricate, convolute, and/or intermediate in arrangement, generally elliptic to obovate, red, orange, or yellow to white sometimes tinged with pink or violet, generally held erect at anthesis, at apex rounded and generally cucullate, thickened at base, entire, often with evident reticulate venation; *stamens* (8)10 [or 15, *A. robertsoniorum*, Léonard, 1986] in 1 or 2 whorls, or rarely reduced to 5 and alternate with petals (*A. hamatus*); filaments shortly fused at base and adnate to bases of petals, equal or dimorphic with two lengths, fil-

aments in outer whorl opposite to petals and sometimes shorter than those of inner whorl, filaments of inner whorl alternate to petals; anthers dithecal and tetrasporangiate, basifixed, oblong, introrse, opening by longitudinal slits, thecae usually separated by a well-developed connective, anthers generally all similar in size even when filaments are dimorphic; pollen 2(4)-colporate; *ovary* inferior or partially inferior, obconic to turbinate, 3-carpellate, 1-locular; styles 1 or usually 3, stigmas 3, oblate to capitate or depressed-globose; ovule 1, basilateral, hemitropous, bitegmic. *Fruit* a turbinate to obconic or oblate nut, indehiscent, dry, smooth to variously ridged or winged, with receptacle often becoming swollen to corky inside perianth scar, 4–5 mm diam., with persistent style base conical, 1–5 mm high, with accrescent sepals becoming enlarged, subequal and coriaceous to chartaceous or markedly unequal, papery, and wing-like; seed 1, endosperm hard, starchy, at least sometimes ruminate with testa intruding between folds; embryo with germination epigeal.

Distribution and habitat. Sixteen species in evergreen forests of tropical Africa and southern India and Sri Lanka through Hainan Island to Sumatra in Asia, 0–1524 m.

Key to Species of *Ancistrocladus*

1a. Plants with flowers [not keyed: *A. griffithii*, *A. tanzaniensis*].
  2a. Sepals 4 or 5, [6.5–9.0]9.5–14.2 mm long; petals 4 or 5, [9.0–]9.5–12.0 mm long . . . . . 6. *A. grandiflorus*
  2b. Sepals 5, 2.0–9.0 mm long; petals 5, 2.0–11.0 mm long.
    3a. Stamens 5; plants of Sri Lanka . . . . . 9. *A. hamatus*
    3b. Stamens 9 to 15; plants of Africa and Asia, except not in Sri Lanka.
      4a. Style 1, with 3 stigmas; petals shorter than sepals.
        5a. Sepals 2.5–5.0 × 2.0–3.0 mm; petals 2.0–3.0 mm long; anthers ca. 0.5 mm long; filaments dimorphic, 0.5–0.7 or 0.8–1.0 mm long; style 1.0–1.5 mm long; branchlet leaves 5.0–24.9 × 2.2–8.1 cm . . . . . 5. *A. ealaensis*
        5b. Sepals 5.0–9.0 × 3.0–6.0 mm; petals 3.0–4.0 × 3.0–4.0 mm; anthers ca. 1.0 mm long; filaments dimorphic, ca. 0.4 or ca. 1.2 mm long; style 2.0–3.0 mm long; branchlet leaves 8.0–50.0 × 3.0–13.0 cm . . . . . 13. *A. likoko*
      4b. Styles 2 or 3, each with 1 stigma [condition unknown in *A. heyneanus*]; petals shorter than, about equal to, or a little longer than sepals.
        6a. Longest filaments 4.0–6.0 mm long.
          7a. Sepals 4.0–9.0 mm long; plants of tropical Asia . . . . . 2. *A. attenuatus*
          7b. Sepals 2.5–5.1 mm long; plants of Africa.
            8a. Adult leaves with small pits frequent to dense on both surfaces (i.e., 1 to 4 per areole formed by tertiary veins); corolla aestivation convolute or intermediate; filaments markedly dimorphic, the shorter ones 1.2–2.0 mm long and about half as long as the longer, these 2.0–4.0 mm long; anthers 0.4–0.7 mm long . . . 3. *A. barteri*
            8b. Adult leaves with small pits sparsely scattered on abaxial surface, sparsely distributed and concentrated near midrib and margins on adaxial surface; corolla aestivation imbricate; filaments slightly dimorphic, the shorter ones ca. 4.5 mm long and ca. 10% shorter than the longer, these ca. 5.0 mm long; anthers 0.8–1.0 mm long . . . . . 8. *A. guineensis*
        6b. Longest filaments 0.7–3.9 mm long.
          9a. Sepals without abaxial glands.
            10a. Branchlet leaves with intramarginal vein situated 2–4 mm from margin; peduncle 4.0–13.0 cm long; inflorescence bracts 0.5–1.0 × 0.2–0.4 mm; sepals unequal, the smaller ones 2.5–3.5 mm long; petals 2.0–3.0 mm long . . . . . 11. *A. korupensis*
            10b. Branchlet leaves with intramarginal vein situated 0–1 mm from margin; peduncle 1.0–4.5 cm long; inflorescence bracts 1.0–1.7 × 1.0 mm; sepals subequal, all 4.0–7.0 mm long; petals 5.0–7.0 mm long . . . . . 14. *A. robertsoniorum*
          9b. External 2 or 3 sepals of some or all flowers with 1 to several abaxial glands.
            11a. Filaments equal or subequal in length, 1.0–1.5 mm long.
              12a. Petals ca. 4.0 mm long; plants of Africa . . . . . 4. *A. congolensis*
              12b. Petals 6.0–7.0 mm long; plants of India . . . . . 10. *A. heyneanus*
            11b. Filaments clearly dimorphic and alternating in length, the shorter ones 0.3–2.0 mm long and the longer ones 0.7–3.9 mm long.
              13a. Petals 2.0–3.0 mm long; longer filaments 0.7–1.3 mm long.
                14a. Branchlet leaves oblanceolate, with L/W 2.9–4.2; sepals unequal, the two shorter 2.5–3.5 mm long and the three longer 5.0–6.0 mm long; bracts of inflorescences at anthesis triangular to narrowly ovate, not elongated at base; stems smooth . . . . . 11. *A. korupensis*
                14b. Branchlet leaves narrowly oblanceolate to elliptic-oblanceolate, with L/W 3.5–15.5; sepals subequal, 2.0–3.0 mm long; bracts of inflorescences

at anthesis spathulate, elongated at base; stems smooth or with small epidermal protuberances . . . . . 12. *A. letestui*

13b. Petals 5.0–11.0 mm long; longer filaments 1.1–3.9 mm long.

15a. Sepals markedly unequal, the smaller two 3.2–4.5 mm long and the larger three 4.2–5.5 mm long; plants of Asia . . . . . 16. *A. tectorius*

15b. Sepals subequal to somewhat unequal, 2.5–6.0 mm long; plants of Africa.

16a. Adult leaves drying at least a little discolorous, dark brown above, yellow-brown beneath; branchlet leaves obovate to elliptic or oblanceolate, with L/W 2.4–4.2; peduncle 4.0–9.5 cm long; petals 2.0–2.5 mm wide; stamens with shorter filaments 1.2–2.0 mm, longer filaments 2.0–4.0 mm, anthers 0.4–0.7 mm long; styles 3.0–4.5 mm long . . . . . 3. *A. barteri*

16b. Adult leaves drying nearly concolorous, yellowish brown to dark brown on both sides or sometimes somewhat reddish brown beneath; branchlet leaves elliptic to obovate, oblong-oblanceolate, or subspathulate, with L/W 1.3–3.6; peduncle 0–2.1 cm long; petals 3.5–6.5 mm wide; stamens with shorter filaments 0.8–1.2 mm, longer filaments 1.2–2.0 mm, anthers 1.0–1.5 mm long; styles 2.5–3.0 mm long . . . . . 1. *A. abbreviatus*

17a. Inflorescence apparently terminal, subsessile or with peduncle to 0.5 cm long, with branched portion 1–3 × 1.5–5.0 cm . . . . . 1a. *A. abbreviatus* subsp. *abbreviatus*

17b. Inflorescence lateral, with peduncle 1.0–2.1 cm long, with branched portions 4.0–5.0 × 6.0–7.0 cm . . . . . 1b. *A. abbreviatus* subsp. *lateralis*

1b. Plants with fruits [not keyed: *A. barteri*, *A. grandiflorus*].

18a. Fruit with accrescent sepals subequal to unequal and continuously grading in size, 3–13 mm long, drying woody to coriaceous or chartaceous, spathulate to oblong, obovate, or oblanceolate.

19a. Nut portion of fruit 4–6 × 7–10 mm.

20a. Accrescent sepals spathulate to obovate or oblong; branchlet leaves 5.0–24.9 × 2.2–8.1 cm, with L/W 2.5–4.3; plants of Africa . . . . . 5. *A. ealaensis*

20b. Accrescent sepals oblanceolate; branchlet leaves 10.0–30.0 × 1.5–4.3 cm, with L/W 4.3–11.5; plants of Asia . . . . . 7. *A. griffithii*

19b. Nut portion of fruit 8–18 × 10–20 mm.

21a. Fruit with accrescent sepals erect to ascending . . . . . 1. *A. abbreviatus*

22a. Infructescence apparently terminal, subsessile or with peduncle to 0.5 cm long, with branched portion 1–3 × 1.5–5.0 cm . . . . . 1a. *A. abbreviatus* subsp. *abbreviatus*

22b. Infructescence lateral, with peduncle 1.0–2.1 cm long, with branched portion 4.0–5.0 × 6.0–7.0 cm . . . . . 1b. *A. abbreviatus* subsp. *lateralis*

21b. Fruit with accrescent sepals spreading.

23a. Margins of accrescent sepals decurrent on fruit body, strongly thickened into 10 stout ridges, the sides deeply sculpted (Fig. 1H, I) . . . . . 13. *A. likoko*

23b. Margins of accrescent sepals decurrent on fruit body but flattened to somewhat thickened into 5 to 7 low ridges, the sides planar to gently concave.

24a. Branchlet leaves 26.0–45.0 × 3.4–5.4 cm, with L/W 6.9–10.3; plants of Asia . . . . . 2. *A. attenuatus*

24b. Branchlet leaves 5.1–40.0 × 2.4–12.5 cm, with L/W 1.3–3.6; plants of Africa.

25a. Infructescence with peduncle 1.0–2.1 cm long; fruit with accrescent sepals triangular with revolute margins . . . . . 1b. *A. abbreviatus* subsp. *lateralis*

25b. Infructescence with peduncle 3–9 cm long; fruit with accrescent sepals spathulate to oblong . . . . . 4. *A. congolensis*

18b. Fruit with accrescent sepals markedly enlarged, unequal, the larger ones 22–56 × 5–25 mm, coriaceous or chartaceous to papery, spathulate to oblanceolate (e.g., Fig. 1F, G).

26a. Nut portion of fruit 10–20 × 9–19 mm.

27a. Nut portion of fruit 20 × 15–19 mm; larger fruiting sepals 22–40 mm long; plants of Sri Lanka . . . . . 9. *A. hamatus*

27b. Nut portion of fruit 10–12 × 9–12 mm; larger fruiting sepals 34–48 mm long; plants of Africa.

28a. Branchlet leaves oblanceolate, with L/W 2.9–4.2; infructescence with peduncle 4.0–13.0 cm long, branched portion 7–16 × 12–20 cm; fruiting sepals chartaceous to papyraceous; plants of Cameroon and Nigeria . . . . . 11. *A. korupensis*

28b. Branchlet leaves oblanceolate to narrowly so, with L/W 4.0–5.8; inflorescence with peduncle 1.1–3.5 cm long, branched portion 3.5–8 × 6–11 cm; fruiting sepals subcoriaceous; plants of Tanzania . . . . . 15. *A. tanzaniensis*

26b. Nut portion of fruit 5–9 × 3–10 mm.

29a. Plants of Asia.

30a. Larger fruiting sepals 25–40 × 12–17 mm, smaller fruiting sepals 19–26 × 5–7 mm; plants of Indian subcontinent . . . . . 10. *A. heyneanus*

30b. Larger fruiting sepals 30–56 × 10–25 mm, smaller fruiting sepals 20–40 × 5–19 mm; plants of Asia east of Indian subcontinent . . . . . 16. *A. tectorius*

29b. Plants of Africa.

31a. External sepals without abaxial glands; plants of coastal forests of east Africa . . . . . 14. *A. robertsoniorum*

31b. External sepals of some or all flowers with marginate abaxial glands (visible at least in young fruits); plants of wet forests of west and central Africa.

32a. Branchlet leaves oblanceolate to obovate, with L/W 2.3–4.8; smaller fruiting sepals 5–16 × 4–6 mm; inflorescence bracts triangular-ovate, not elongating by late anthesis, remaining 0.8–1.6 mm long; stems smooth . . . . . 8. *A. guineensis*

32b. Branchlet leaves narrowly oblanceolate to elliptic-oblanceolate, with L/W 3.5–15.5; smaller fruiting sepals 21 × 8–10 mm; inflorescence bracts lanceolate to triangular-oblanceolate at early anthesis, elongating by late anthesis to 3.0–3.5 mm and becoming cochleate to clavate; stems smooth or with small epidermal protuberances . . . . . 12. *A. letestui*

1. Ancistrocladus abbreviatus Airy Shaw, Kew Bull. 1949: 67. 1949. TYPE: Sierra Leone. Southern Prov.: Njala, 5 Jan. 1933, *F. C. Deighton 2589* (lectotype, designated by Airy Shaw (1950: 148), K!; syntypes, BM!, P!).

Juvenile plants unknown. *Juvenile leaves* unknown. *Adult stems* climbing to 10 m high, to 10 mm diam. [probably becoming larger but no data], with bark gray to purplish brown, smooth to roughened or longitudinally fissured, bearing some scattered leaves and apparently rather numerous lateral branchlets to 30 cm long, these each bearing 1 to several hooks and a terminal group of leaves; *hooks* recurved to spiraling, (5–)10–19 mm diam. *Adult leaves* drying chartaceous to subcoriaceous, dull to rather shiny on both surfaces, in life dark green on adaxial surface, paler on abaxial surface, drying nearly concolorous, yellowish brown to dark brown on both surfaces or sometimes somewhat reddish brown on abaxial surface; pits dimorphic, small pits moderately densely distributed to frequent on both surfaces or sometimes only evident on adaxial surface, large pits 0.2–0.5 mm diam., circular, few and scattered on adaxial surface, sometimes arranged in a sparse row parallel to midrib, rarely a few on abaxial surface; midrib adaxially plane or a little thickened, abaxially prominulous to prominent, terminating in a tiny gland or this sometimes displaced to below leaf apex; secondary veins prominulous on both surfaces but usually more so abaxially; tertiary veins reticulated and similarly prominulous on both surfaces; margins thickened and cartilaginous throughout, plane or usually narrowly revolute along sides of blade; *stem leaves* with persistence unknown, elliptic-obovate to elliptic, 12.7–20.5(–34.1) × (3.6–)6.4–8.8 cm, L/W 2.0–2.4, at apex obtuse to rounded, at base cuneate to acute; secondary veins 8 to 10 pairs; *leaves at branchlet apices* with persistence unknown, elliptic to obovate, oblong-oblanceolate, or subspathulate, (5.1–)10.5–40.0 × (2.4–)4.0–12.5 cm, L/W (1.3–)2.0–3.6, at apex very shortly obtusely acuminate to obtuse to rounded or truncate, at base acute to cuneate and usually long-tapered then shortly abruptly rounded to truncate; secondary veins 5 to 10(to 14) pairs, with intramarginal vein situated 4–5 mm from margin. *Inflorescence* subcapitate to congested-cymose or paniculate, lateral or apparently terminal among leaves on branchlets, without hooks or bracteal leaves, subsessile or with peduncle to 2.1 cm long; branched portion subglobose to broadly pyramidal or corymbiform, 1–5 × 1.5–7.0 cm, dichotomously branched; bracts ovate to oblong-ovate or triangular, 0.5–1.5 × 1.0–1.2 mm long, at apex obtuse to acute, entire to a little erose and scarious, at base obtuse to rounded, abaxially eglandular or with 1 to 2 circular glands in basal portion; pedicels 1–5 mm long. *Flowers* all pedicellate; *sepals* 5, elliptic to obovate or suborbicular, rounded and a little cucullate at apex, at base cuneate to acute and shortly decurrent on ovary, color unknown, abaxially with 2 to 6 circular to compressed glands, adaxially rather densely and finely punctate, somewhat unequal, 3.0–6.0 × 2.5–4.1 mm; *petals* 5, convolute, obovate to suborbicular, yellow to white, cream, or pink, (6.0–)9.0–10.0 × (3.5–)5.0–6.5 mm; *stamens* 10 apparently in 1 whorl, white; filaments slender, dimorphic, the shorter 0.8–1.2 mm long, the longer 1.2–2.0 mm long; anthers 1.0–1.5 mm long; *ovary* fully inferior, ca. 2 mm long; styles 3, 2.5–3.0 mm long, stigmas ca. 0.3 mm long. *Fruit* turbinate; nut 8–15 × 10–15 mm, on sides longitudinally 5-ridged by thickened decurrent margins of accrescent sepals; persistent sepal limbs ascending or spreading, spathulate, coriaceous drying woody, unequal, 3–8 × 3–5 mm, flat, rounded to triangular, with revolute margins; pericarp perhaps coriaceous, drying woody, chestnut brown; seeds not seen.

Distribution, phenology, and habitat. Wet evergreen forests on river banks and river islands at 130–160 m, Sierra Leone to Nigeria; for phenology see individual subspecies, below.

Provisional conservation status. Each subspecies is assessed separately, below.

Airy Shaw (1949) in his original description noted that plants of *Ancistrocladus abbreviatus* are scandent or perhaps shrubs, with a question mark as to this latter habit; field notes on the specimen *Hall & Enti GC-39985* (GC) do describe the plant as a shrub. Airy Shaw (1949: 68) described the bracts as "1.5 cm long," but this appears to be a typographical error: they are ca. 1.5 mm long on the type collection and of similar size on the other specimens examined. Several specimens included in *A. abbreviatus* by Airy Shaw were previously treated by Scott-Elliot as *A. barteri*; see the discussions below under *A. abbreviatus* subsp. *lateralis* and *A. barteri*.

The leaf margins of this species are notably thickened and cartilaginous, and the leaves are obtuse to usually rounded or even truncate at their apices, rather than clearly angled to acute or acuminate as in most other species of *Ancistrocladus*. The leaves dry generally concolorous and usually with a dark brown color, rather than markedly discolorous with the lower surfaces quite pale as in most other African *Ancistrocladus* species. *Ancistrocladus likoko* is generally similar in these leaf features as well as in having relatively short and thick-textured accrescent sepals on the fruits, but can be separated by several characters as noted in the keys presented above and in Appendix I. The collections studied of *A. abbreviatus* all note that the plants were growing on riversides, and it seems likely that its fruits with their stout, relatively short accrescent sepals are adapted for water dispersal. Bringmann et al. (1990) and Manfredi et al. (1991) studied alkaloids found in *A. korupensis*, but their study material was incorrectly identified as "*A. abbreviatus*" and their results incorrectly attributed to this species (Foster & Sork, 1997).

1a. Ancistrocladus abbreviatus Airy Shaw subsp. **abbreviatus**

Leaves at branchlet apices relatively broad, with L/W (1.3–)2.0–3.1, obtuse to rounded or truncate at apex. *Inflorescence* apparently terminal, subcapitate to congested-cymose; subsessile or with peduncle to 0.5 cm long; branched portion 1–3 × 1.5–5.0 cm. *Fruit* with persistent sepal limbs ascending, flat, rounded.

Distribution, phenology, and habitat. Wet evergreen forests on river banks and river islands at 130–160 m, Sierra Leone to Ghana; collected in flower in January, November, and December, in fruit in May and December.

Provisional conservation status. With an EO greater than 20,000 km² and existing in Ghana, Guinea (i.e., Guinea-Conakry), Côte d'Ivoire (i.e., Ivory Coast), Liberia, and Sierra Leone: Least Concern; Cheek (2000: 876) also proposed a status of Lower Risk, Least Concern (LR/lc) for the species as a whole.

This subspecies comprises most of the collections seen of this species.

Selected specimens examined. COTE D'IVOIRE. **Bas Sassandra:** in Sassandra River betw. Péhiri & Kopréagui, ca. 7 km WNW of Soubré, *de Wilde 3314* (BR, P, WAG [2]); 2 km N of Taï, rt. bank N'Cé River, *Leeuwenberg 3036* (WAG [3]). GHANA. **Ashanti/Brong-Ahafo border:** near River Tano, ca. 75 km W of Kumasi, *Oldeman 838* (BR, FHI, MO, P, WAG [2]). **Eastern/Greater Accra:** River Densu off Amasamang, *Enti FE-1906* (MO [2], US, WAG [2]). GUINEA [GUINEA-CONAKRY]. **Kindia:** Kolente, *Chillou 984* (P), *Lisowski 51512* (BR). LIBERIA. **Central:** Salala Dist., along St. Paul River, *Baldwin 10603* (MO, US [2], WAG). SIERRA LEONE. **Northern:** Kambi, Scarcies, *Scott-Elliot 4384* (GH).

1b. Ancistrocladus abbreviatus Airy Shaw subsp. **lateralis** Gereau, subsp. nov. TYPE: Nigeria. Anambra State: "East Central State," Awka Dist., Mamu Forest Reserve, 6 Nov. 1973, *J. A. Emwiogbon 344* (holotype, FHI-72100!; isotype, FHI-94497!).

Ancistrella barteri Tiegh., J. Bot. (Morot) 17: 155. 1903, not *Ancistrocladus barteri* Scott-Elliot. TYPE: Nigeria. Anambra State: Onitsha, 1858, *C. Barter 1699* (holotype, P!; isotype, K!).

Haec subspecies ab *A. abbreviato* subsp. *abbreviato* inflorescentia laterali pedunculo extra-axillari 1.0–2.1 cm longo insidente parte ramificante corymbiformi 4–5 cm longa, 6–7 cm lata atque fructu cum sepalorum limborum partibus apicalibus liberis patentibus triangularibusque distinguitur.

Leaves at branchlet apices relatively narrow, with L/W 2.5–3.6, very shortly and obtusely acuminate to rounded at apex. *Inflorescence* lateral, paniculate; peduncle 1.0–2.1 cm long; branched portion 4–5 × 6–7 cm. *Fruit* with persistent sepal limbs spreading, triangular, with revolute margins.

Distribution, phenology, and habitat. In wet forests, swamp forests, and seasonal swamps at ca. 5–200 m, Nigeria, collected in flower in November and December, in fruit in December, February, and May.

Provisional conservation status. With distribution restricted to southern Nigeria where forest ex-

tent both inside and outside forest reserves continues to suffer extreme decline in quality of habitat due to agricultural encroachment: Critically Endangered (A2c).

This new subspecies comprises a geographically disjunct population, or set of populations, that clearly belong to *Ancistrocladus abbreviatus* but are morphologically distinct in a few features. Airy Shaw (1949) included these plants in *A. abbreviatus* without comment, but they differ in their inflorescence position and arrangement. This new subspecies includes several collections (in particular *Barter 1699*) previously included by Scott-Elliot in *A. barteri*; see also the discussion under that species. When Airy Shaw (1950) lectotypified *A. barteri* he chose a different specimen, *Scott-Elliot 4860,* in spite of the eponymy given that species by Scott-Elliot in his original description.

Paratypes. NIGERIA. **Anambra:** Onitsha prov., 2 mi. from Hinata on path to Nnani, *A. P. D. Jones 2715 or FHI-621* (FHI, P). **Cross River:** Lower Enyong Forest Reserve betw. pillars 33 & 34 of Obio Usiere Reserve boundary, *D. A. Ibeneghu & Forest Guard FHI-26206* (FHI, P); Ikot Efa Beach, Uwet-Odot For. Res., *C. F. A. Onochie FHI-33233* (FHI). **Rivers:** Kabba, Igala, *A. P. D. Jones 2807 or FHI-5898* (FHI); ca. 1 mi. to Imo River village on Port Harcourt-Aba Road, *C. F. A. Onochie FHI-40443* (FHI).

2. Ancistrocladus attenuatus Dyer, in Hook. f., Fl. Brit. India 1: 300. 1874. TYPE: India and Myanmar [Burma]. "Tenasserim and Andaman Islands," s.d., *J. W. Helfer s.n. in Kew Distrib. "Herbarium of the Late East Indian Company" 724* (lectotype, designated by Gereau (1997: 243), K not seen, photo MO!; isotypes, C!, GH!, K!, L!, P [2]!).

Juvenile plants unknown. *Juvenile leaves* unknown. *Adult stems* with height not noted, to 10 mm diam. [probably becoming larger but no data], with bark purplish brown, smooth to roughened, bearing some scattered leaves, lateral branchlets of unknown length, and sometimes a terminal rosette of leaves, lateral branches bearing terminal groups of leaves; *hooks* not seen. *Adult leaves* drying papyraceous to chartaceous, dull on both surfaces, in life not seen, drying discolorous, dark brown adaxially, pale brown or yellow-brown abaxially; pits dimorphic, small pits moderately densely distributed to frequent on both surfaces or sometimes only found on adaxial surface, large pits 0.3–0.5 mm diam., circular or elliptic, few and scattered on abaxial surface; midrib adaxially shallowly sulcate, abaxially prominent, terminating in a tiny gland; secondary veins plane on adaxial surface, very slightly prominulous on abaxial surface; tertiary veins reticulated on both surfaces; margins plane; *stem leaves* not seen; *leaves at branchlet apices* with persistence unknown, lanceolate or oblanceolate, 26.0–45.0 × 3.4–5.4 cm, L/W 6.9–10.3, at apex acute and sometimes abruptly shortly acuminate, at base narrowly cuneate to long-attenuate; secondary veins 11 to 20 pairs, with intramarginal vein situated 3–5 mm from margin. *Inflorescence* lax, paniculate, lateral among leaves at apices of branchlets, without hooks or bracteal leaves; peduncle 2.5–7.5 cm long, stout; branched portion corymbiform, 7–18 × 6–23 cm, dichotomously branched; bracts triangular, ca. 0.7 × 0.5 mm, hyaline, at apex acute, at base obtuse, abaxially with a gland covering ⅓–⅔ of surface; pedicels ca. 1.0 mm long. *Flowers* all pedicellate, not seen, description based on Das (1993); *sepals* 5, unequal, 4.0–9.0 × 2.0–3.0 mm; *petals* 5, arrangement unknown, obovate-oblong, white, 5.0–9.0 × 3.0–5.0 mm; *stamens* 10, arrangement unknown; filaments pyramidal, whether dimorphic unknown, 4.0–6.0 mm long; anthers ca. 1.0 mm long; *ovary* fully inferior, size unknown; styles 3, size unknown, stigmas not seen. *Fruit* turbinate; nut ca. 10 × 14 mm, on sides longitudinally shallowly 5-ridged by decurrent margins of accrescent sepals; persistent sepal limbs chartaceous to coriaceous, their free apical parts spreading, spathulate, equal to a bit unequal, 8–15 × 5–8 mm; pericarp drying dull brown, coriaceous to chartaceous; *seed* not seen.

Distribution, phenology, and habitat. Evergreen scrub and bamboo forests at 50 m, India, Burma, and Andaman Islands; collected in fruit in June.

This species is similar to *Ancistrocladus griffithii* in its small scattered bracts, and to *A. tectorius* in its petals that are markedly longer than its sepals (e.g., *Helfer s.n.*). The lectotype specimen of *A. attenuatus* has young fruits that generally resemble those of *A. griffithii,* except the fruits of *A. griffithii* have the nut portion smaller (5–6 × 8–10 mm) and the persistent sepal limbs often somewhat smaller (5–12 × 4–6 mm). The fruits of *A. attenuatus* also resemble the fruits of *A. hamatus,* except the fruits of *A. hamatus* have strongly unequal persistent sepal limbs. The few fruits seen of *A. attenuatus* may of course be immature.

The name *Ancistrocladus wallichii* Planch. has been applied to plants similar to *A. attenuatus.* However, the type specimens of *A. wallichii* show a wide range of leaf sizes and shapes and lack flowers and fruits. Consequently, the identity of *A. wallichii* is not clear, and this is treated as a name of dubious identity.

Selected specimens examined. INDIA. **West Bengal:** Bengalia near Calcutta, *J. W. Helfer s.n.* (A, P, PNH). MYANMAR [BURMA]. [Probably] **Mon:** "Singkuwm," Tenasserim, *A. F. G. Kerr 21661* (BM).

3. Ancistrocladus barteri Scott-Elliot, J. Linn. Soc., Bot. 30: 73. 1894. TYPE: Sierra Leone. Not located as to region: Mount Gonkwi, Duunia, Talla Hills, 16 Feb. 1892, *G. F. Scott-Elliot 4860* (lectotype, designated by Airy Shaw (1950: 148), K!; isotype, BM!).

Ancistrocladus pachyrrhachis Airy Shaw, Kew Bull. 1950: 149. 1950. Syn. nov. TYPE: Liberia. Montserrado County: Monrovia, 30 May 1947, *J. T. Baldwin Jr. 5839* (holotype, K [sheet 1 of 4]!; isotypes, K [sheets 2–4 of 4]!).

Juvenile plants very slender saplings to 2 m tall, lacking hooked branchlets. *Juvenile leaves* with persistence unknown, oblanceolate, 36.7–59.6 × 8.4–12.0 cm, L/W 4.4–5.0, at apex obtuse to acute, at base acute then attenuate then abruptly very shortly rounded or long-attenuate (i.e., pseudopetiolate), in life not seen, drying chartaceous, dull or shiny, discolorous, brown above, yellowish brown below; pits similar to those of adult leaves; midrib plane adaxially, thinly prominulous to prominent abaxially, with terminal gland not found; secondary veins 12 to 17 pairs; secondary and tertiary veins prominulous adaxially and abaxially; margins plane to thinly revolute. *Adult stems* climbing to 15 m high, to 8 mm diam. [probably becoming larger but no data], with bark gray-brown, smooth or with shallow longitudinal fissures, bearing scattered leaves and lateral branchlets to 50 cm long, these branchlets bearing a terminal group of leaves, without hooks (e.g., *Hall & Aké Assi GC-45772,* GC) or with 1 to several hooks (e.g., *Morton & Gledhill SL 1027,* WAG); *hooks* recurved to spiraling, 6–25 mm diam. *Adult leaves* drying chartaceous to stiffly subcoriaceous, rather shiny on both surfaces, in life discolorous, dark green above, light green below, drying at least a little discolorous, dark brown above, yellow-brown below; pits dimorphic, small pits frequent to dense on both surfaces (i.e., 1 to 4 per areole formed by tertiary veins), large pits 0.1–0.3 mm diam., circular, widely scattered on both surfaces (i.e., several per leaf); midrib adaxially plane to shallowly sulcate, abaxially prominent, often terminating in a tiny gland; secondary veins prominulous on both surfaces; tertiary veins reticulated and prominulous on both surfaces; margins very thinly revolute; *stem leaves* with persistence unknown, elliptic to oblanceolate or narrowly obovate, 6.3–41.7 × 2.4–10.6 cm, L/W 2.6–4.6, at apex rounded to short-acuminate, at base cuneate to truncate; secondary veins 5 to 20 pairs, with submarginal vein situated 2–5 mm from margin; *leaves at branchlet apices* with persistence unknown, obovate to elliptic or oblanceolate, 3.5–31.4 × 1.8–9.4 cm, L/W 2.4–4.2, at apex rounded or obtuse to acute or acuminate with acumen to 15 mm long, at base cuneate to acute then abruptly and very shortly rounded, sometimes basally narrowly long-attenuate (i.e., pseudopetiolate); secondary veins 5 to 14 pairs, with intramarginal vein situated 3–6 mm from margin. *Inflorescence* lax, paniculate, lateral among leaves at apices of branchlets, without hooks, sometimes with bracteal leaves similar to adult stem leaves (e.g., *Aké Assi 17146,* MO; *Baldwin 10984,* MO; *Merello et al. 1301,* MO); peduncle 4.0–9.5 cm long, straight to curved; branched portion corymbiform, 5–15(–24) × 7–16 cm, branched 1 to 4 times dichotomously then subsequent axes racemiform; bracts ovate to triangular, 1–2 mm long, at apex acute to obtuse, at base obtuse, marginally hyaline and often erose, abaxially with a rounded gland covering ½–⅔ of surface; pedicels 1–4 mm long. *Flowers* all pedicellate; *sepals* 5, narrowly elliptic to elliptic-oblong, rounded and entire at apex, at base cuneate to obtuse and decurrent on ovary, green sometimes with translucent veins and/or red margins, external 2 or 3 sepals abaxially with 1 to 4 elliptic raised glands, adaxially apparently without pits, subequal, 2.5–4.5 × 1.5–3.0 mm; *petals* 5, convolute or rarely intermediate (e.g., *Leeuwenberg 2709,* WAG), obovate, yellowish white or white tinged pink or sometimes pale violet internally and orange externally, 5.0–11.0 × 2.0–2.5 mm; *stamens* 9 or 10 in apparently 2 whorls, white; filaments slender, dimorphic, the shorter 1.2–2.0 mm long, the longer 2.0–4.0 mm long; anthers 0.4–0.7 mm long; *ovary* fully inferior, ca. 2 mm long; styles 3, 3.0–4.5 mm long, stigmas 0.2–0.5 × 0.5–0.8 mm. *Fruit* not seen.

Distribution, phenology, and habitat. Lowland wet forests from sea level to 95 m, on coastal bluffs, along rivers, and in a laterite pit, Senegal to Ghana; collected in flower December through March, in fruit in February.

Provisional conservation status. With an EO greater than 20,000 km^2 and existing in Côte d'Ivoire (i.e., Ivory Coast), Ghana, Guinea (i.e., Guinea-Conakry), Guinea-Bissau, Liberia, Senegal, and Sierra Leone: Least Concern; Cheek (2000: 881) proposed a status of Data Deficient (DD).

In floral characters, *Ancistrocladus barteri* is distinguishable from *A. guineensis* only by corolla aestivation, degree of dimorphism of filaments, and stamen dimensions, as outlined in the Key to Spe-

cies above. These two species (or geographical populations) also seem distinguishable by leaf characters: numerous obvious small pits are found throughout the leaves of *A. barteri*, versus few to frequent but hardly visible small pits restricted to the leaf undersurface and sometimes also isolated zones on the upper surface of the leaves of *A. guineensis*. However, with very few collections of these species available at anthesis, the occurrence of intermediate as well as convolute corolla aestivation in *A. barteri* makes their distinction somewhat tenuous. These two species are provisionally maintained here based on the characters noted above and their apparently allopatric geographic ranges, but their status will need re-evaluation when fruits are discovered for *A. barteri*.

No fruiting collections can be confidently associated with *Ancistrocladus barteri*. Scott-Elliot (1894: 73–74) described the fruits briefly in his original description as "obpyramidale, 5-angulare, costis incrassatis, sine calycis lobis 15 mm. long. et 15 mm. lat." However, the specimen on which this description is based is unknown and may be among those treated here as *A. abbreviatus*. In his original circumscription of *A. barteri*, Scott-Elliot included several specimens that were subsequently excluded from *A. barteri* by Airy Shaw (1949), who referred most of them to his newly described species *A. abbreviatus*. *Ancistrocladus abbreviatus* does have fruits that correspond to Scott-Elliot's description.

Scott-Elliot (1894) did not designate a type for *Ancistrocladus barteri*, but listed a set of syntypes. As noted by Gereau (1997), Airy Shaw later (1950) re-evaluated *A. barteri*, restricting its circumscription and selecting a lectotype, *Scott-Elliot 4860* from Sierra Leone. Scott-Elliot (1894: 74) specifically listed under his *A. barteri* the Nigerian specimen *Barter 1699*, whose identity has been controversial. Airy Shaw later (1949) identified this as *A. guineensis*, Keay (1954) subsequently included it in *A. abbreviatus*, and it is here included in the newly described *A. abbreviatus* subsp. *lateralis*. This was the only Barter collection included by Scott-Elliot in this eponymous species, but Airy Shaw explicitly excluded this Barter collection from his circumscription of *A. barteri* without explanation. However, there are no nomenclatural grounds on which to overturn Airy Shaw's decision.

Separately Tieghem (1903: 154) stated that *Barter 1699* had characters that distinguished it from all other Ancistrocladaceae, and gave it the provisional name "*Ancistrocladus barteri* Tiegh." He explained his conclusion as follows: "C'est donc au bien, tout au moins, une espèce autonome, que je nommerai pour le moment A. de Barter (*A. Barteri* v.T.)." In the same article, Tieghem (1903: 155) also published the new genus *Ancistrella* Tiegh. with the single species *Ancistrella barteri* Tiegh., based on *Barter 1699*, and asserted that this second name was the one he intended to accept: ". . . on est conduit à regarder cette plante comme le type d'un genre nouveau, que je nommerai Ancistrelle (*Ancistrella* v.T.). Ce sera désormais l'Ancistrelle de Barter (*Ancistrella Barteri* v.T.)." Tieghem (1903) analyzed the leaf anatomy of *Ancistrella barteri* in great detail and must have derived his anatomical material from the specimen *Barter 1699*, which was distributed to P apparently with Scott-Elliott's name on it. In any case Tieghem, with his particular interest in *Ancistrocladus*, was probably aware of the publication of Scott-Elliot's name. Unfortunately, Tieghem (1903) was not always clear or conventional in his use of taxonomic nomenclature, so his intent is not entirely clear here. However, his use of his own initials with these names seems to indicate that his intent was indeed to separate these names from Scott-Elliot's usage. Therefore, Tieghem's work cannot be interpreted as a lectotypification of Scott-Elliot's name, and the names *Ancistrocladus barteri* Scott-Elliot and *Ancistrella barteri* Tiegh. are heterotypic and independent due to the lectotypification of *Ancistrocladus barteri* by Airy Shaw (1950).

As circumscribed here, *Ancistrocladus barteri* is variable in leaf size and shape, inflorescence size, petal size, and filament length. However, the specimens included here are linked by a continuous range of variation in these features, as discussed below. In particular, the variation in leaf form can be generally separated into several rather well-marked groups. One group is characterized by relatively small, elliptic to obovate leaves that are obtuse to rounded at the apex and contracted in the basal portion to a narrowed, pseudopetiolate structure; specimens with such leaves have petals 6–8 mm long and the longer filaments ca. 2 mm long (these measurements are based on three flowering collections, apparently representing three plants). A second group is characterized by its often larger, oblanceolate leaves that are acute to acuminate at the apex and uniformly narrowed to an acute base; specimens with such leaves have petals 6–11 mm long and the longer filaments ca. 4 mm long (these measurements are based on six flowering collections, representing five plants). The shortest of these petal measurements, 6 mm, is found on the type of *A. barteri*, which has relatively long narrow leaves with shortly acuminate apices.

Several collections of *Ancistrocladus barteri* com-

prise multiple sheets that sample various portions of the plants, and include a wide range of leaf sizes and shapes. In particular a wide range of leaf sizes and shapes, on both sterile and flowering branchlets and ranging from relatively long and narrow to quite small and apically obovate and obtuse, is found in the multi-sheet collection *Baldwin 5839* [K!, the type of *A. pachyrrhachis*; *Baldwin 10984* is taken from the same plant (Airy Shaw, 1950), and shows the same pattern]. The smallest leaves have apparently been considered aberrant, but they are found subtending most of the inflorescences, and are also found on sterile branchlets (e.g., *de Wilde 801*, BR). A notable narrowing to a pseudopetiolate leaf base is seen in *J. G. Adam 23228* (MO) and *Malaisse 14718* (MO), but these collections have acute leaf apices and the second collection has petals ca. 9 mm long. One collection, *Morton & Jarr 1758* (WAG), has leaves that vary from apically obtuse to slightly acuminate and basally attenuate to pseudopetiolate, linking the two leaf forms. A similarly broad variation in leaf size and shape is found in *A. letestui* (e.g., *Hallé 3955*, P).

Ancistrocladus pachyrrhachis was described (Airy Shaw, 1950) based on two collections by Baldwin that were both taken from the same plant and both with infructescence axes from which the fruits have all fallen. These collections are notable in the relatively large inflorescences with the ultimate axes markedly prolonged and racemiform. However, they differ in no other way from collections of *A. barteri*, and the inflorescence size in specimens assigned by Airy Shaw to *A. barteri* actually varies quite widely and reaches a size only a little smaller than that of Baldwin's specimens of *A. pachyrrhachis*. Consequently, *A. pachyrrachis* is here considered a synonym of *A. barteri*.

Selected specimens examined. CÔTE D'IVOIRE. **Lagunes:** near Port Bouêt, E of Abidjan, *Leeuwenberg 2709* (WAG [2]). GHANA. **Western Province:** along Takoradi–Elubo Road, 9.5–23.5 km E of Elubo, 5°10′N, 2°40′W, *Merello et al. 1301* (MO). GUINEA-BISSAU. **Tombali:** Cabum, 11°12′N, 15°08′W, *Malaisse 14718* (MO). LIBERIA. **Loffa:** betw. Zorzor & Voinjama, in Loma Nat. Forest, *Bos 2614* (WAG [2]). SENEGAL. **Ziguinchor:** Basse Casamance, región d'Oussouye, Boukitingo, *Berhaut 7406* (BR, P). SIERRA LEONE. **Northern:** Loma Mts., Kondambaia to fishing camp, *Morton & Gledhill SL 1027* (FHI, WAG [2]). **Western:** Freetown, Bot. Garden, Fourah Bay College, *Morton & Jarr SL 1758* (FHI, WAG).

4. Ancistrocladus congolensis J. Léonard, Bull. Soc. Roy. Bot. Belgique 82: 33. 1949. TYPE: Democratic Republic of the Congo. Orientale Prov.: Forestier Central, Yafunga sur Zaïre, près d'Isangi, 8 Sep. 1938, *J. Louis 11171* (holotype, BR!; isotypes, BM!, BR!, K not seen, P not seen).

Juvenile plants unknown. *Juvenile leaves* unknown. *Adult stems* climbing to 20 m tall, to 5 cm diam., with bark smooth to shallowly longitudinally fissured, gray-brown to purple-brown or brown, bearing scattered leaves and lateral branchlets to 15 cm long, these each bearing 1 to several hooks and a terminal group of leaves; *hooks* recurved to spiraling, 6–17 mm diam. *Adult leaves* drying subcoriaceous to coriaceous, on both surfaces dull or a little shiny, in life not seen, drying concolorous and dark brown or usually a little discolorous, dark brown above and reddish brown below; pits dimorphic, small pits sparsely to rather densely distributed on both surfaces, large pits 0.2–0.4 mm diam., circular, occasional and scattered on both surfaces; midrib adaxially plane to shallowly sulcate, abaxially prominent, usually terminating in a tiny gland; secondary veins prominulous on both surfaces; tertiary veins reticulated and prominulous on both surfaces; margins plane to thinly revolute; *stem leaves* with persistence unknown, elliptic to broadly elliptic, 9.2–18.0 × 4.8–8.5 cm, L/W 1.8–1.9, at apex obtuse to rounded or truncate, at base cuneate to obtuse; secondary veins 6 or 7 pairs, with intramarginal vein situated 2–5 mm from margin; *leaves at branchlet apices* with persistence unknown, elliptic to elliptic-oblong or broadly elliptic, 7.0–27.8 × 3.0–10.1 cm, L/W 2.0–3.4, at apex obtuse to subacute or rounded to truncate and sometimes abruptly acuminate with the deltoid acumen to 5 mm long, at base acute to obtuse; secondary veins 4 to 14 pairs, with intramarginal vein situated 2–5 mm from margin. *Inflorescence* lax, paniculate, lateral among leaves on branchlets, without hooks, occasionally bearing bracteal leaves similar to adult stem leaves (e.g., *Hallé & Le Thomas 287*, P); peduncle 3–8[–9, Léonard, 1949] cm long, rather stout; branched portion corymbiform, 4.0–5.5[–14, Léonard, 1949] × 5.5–12.0[–13, Léonard, 1949] cm, dichotomously branched, axes sometimes rather stout; bracts ovate to triangular or lanceolate, 0.5–2.0 mm long, at apex acute to obtuse, at base obtuse, denticulate or short-erose [to entire, Léonard, 1949], abaxially eglandular or larger bracts with a gland covering ⅓–⅔ of surface; pedicels 1.5–4.0 mm long. *Flowers* all pedicellate; *sepals* 5, oblong to obovate, rounded and entire to denticulate or ciliolate at apex, obtuse to rounded at base, pale green, abaxially with 1 to 3 small compressed marginate glands, adaxially apparently papillate but without pits, subequal, [3.0–, Léonard, 1949]5.0–6.0 × 2.0–3.0 mm; *petals* 5, imbricate to

sometimes convolute (*Germain 5049*, BR) or rarely intermediate (*Léonard 1513*, BR), obovate [to broadly ovate, Léonard, 1949], yellow, ca. 4.0 × 3.0–3.5 mm; *stamens* 10 apparently in 1 whorl; filaments apparently equal, ca. 1.5 mm long; anthers ca. 0.5 mm long; *ovary* partially inferior, inferior portion ca. 2 mm long, superior portion ca. 0.5 mm high; styles 3, ca. 1.5 mm long, red-brown, stigmas red, size unknown. *Fruit* turbinate; nut 8–15 × 10–20 mm, on sides longitudinally 5- to 7-ridged by decurrent margins of accrescent sepals, these usually uniting below top of nut; persistent sepal limbs spreading, woody to stiffly chartaceous with texture thinning toward apex, spathulate to oblong, subequal to somewhat unequal, 5–10 × 3–4 mm but apex often breaking off; pericarp orange drying dark brown, woody to corky; *seed* 6–7 mm diam.

Distribution, phenology, and habitat. In swamp and riverine forests, the only elevation noted 470 m, northern Democratic Republic of the Congo and Republic of the Congo to Gabon; collected in flower in October, in fruit in March, April, August, October, and December.

Provisional conservation status. With an EO greater than 20,000 km² and existing in the Democratic Republic of the Congo, Gabon, and the Republic of the Congo: Least Concern; Cheek (2000: 876) also proposed a status of Lower Risk, Least Concern (LR/lc).

This species is similar to *Ancistrocladus ealaensis*, and at least one specimen included in that other species by Léonard (1949) is here treated as *A. congolensis*. In general, plants with leaves that are notably acuminate and/or with leaves that are distinctly broadest well above the middle are here treated in *A. ealaensis* rather than *A. congolensis*.

Léonard described *Ancistrocladus congolensis* as stipulate and illustrated (1949: fig. 1D) a portion of a young stem. This figure shows some structures that are presumably leaf bases along with the purported stipules, figured as small flaps of tissue irregularly distributed along this stem. In this figure some of these leaf bases arise from above the purported stipules, while other leaf bases lack these flap-like structures. Otherwise stipules have not been seen in this species, even on well-preserved stem apices, nor do any of the specimens studied bear stipule scars (e.g., *Louis 16349*, BR), and the structures illustrated by Léonard were not seen on the specimen cited in the figure (*Louis 16776*, BR). However, Léonard did study these plants in the field and presumably had evidence for his statement that this species is stipulate.

Léonard (1949, 1982) described and illustrated galled flowers and fruits of this species, which are found occasionally on herbarium specimens. These galls are similar in form to those of *Ancistrocladus ealaensis* but apparently much less frequent.

Selected specimens studied. DEMOCRATIC REPUBLIC OF THE CONGO. **Orientale:** à 25 km en amont d'Isangi, *Germain 4789* (BR). GABON. **Ngounié/Ogooué-Maritime border:** Rabi-Koung, 1°55′S, 9°55′E, *Breteler & Jongkind 10137* (MO, WAG). REPUBLIC OF THE CONGO. **Pool:** Brazzaville, Chaillu, chutes de Dimani sur la Nyanga, à Divenié, *Sita 4824* (BR).

5. Ancistrocladus ealaensis J. Léonard, Bull. Soc. Roy. Bot. Belgique 82: 30. 1949. TYPE: Democratic Republic of the Congo. Equateur: Forestier Central, environs d'Eala, rivière Yuli, 23 Nov. 1946, *J. Léonard 1057* (holotype, BR!; isotypes, BR!, K!, P!, YBI not seen).

Juvenile plants unknown. *Juvenile leaves* unknown. *Adult stems* climbing to 12 m tall, the main stems to 4 cm diam., with bark smooth to longitudinally shallowly fissured, purple-brown to gray-brown, bearing some scattered leaves and also lateral branchlets to 50 cm long, these each bearing 1 to several hooks and 1 to several groups of leaves; *hooks* recurved to spiraling, 5–17 mm diam. *Adult leaves* drying chartaceous to subcoriaceous, on both surfaces dull to a little shiny, in life not seen, drying discolorous, gray-brown to dark brown above, reddish brown below; pits dimorphic, small pits rather densely distributed on both surfaces, large pits 0.3–0.5 mm diam., circular, occasional and scattered on both surfaces; midrib adaxially flat to shallowly sulcate, abaxially prominulous to prominent, terminating in a tiny gland; secondary veins prominulous on both surfaces; tertiary veins reticulated and prominulous on both surfaces; margins plane to thinly revolute; *stem leaves* with persistence unknown, elliptic to oblanceolate, 3.4–29.1 × 1.6–9.8 cm, L/W 2.1–4.6, at apex acuminate with narrow acumen 5–30 mm long or occasionally obtuse to rounded, at base acute to attenuate or sometimes narrowly contracted (i.e., pseudopetiolate); secondary veins 8 to 15 pairs, with intramarginal vein situated 3–7 mm from margin; *leaves at branchlet apices* with persistence unknown, elliptic, narrowly elliptic, elliptic-oblong, or oblanceolate, 5.0–24.9 × 2.2–8.1 cm, L/W 2.5–4.3, at apex acute to acuminate with tips 3–12[–40, Léonard, 1949] mm long or occasionally obtuse to rather rounded, at base cuneate to acute or rarely abruptly narrowly contracted (i.e., pseudopetiolate), with secondary veins 5 to 12 pairs, with intramarginal vein situated 3–7 mm from margin. *Inflorescence* lax, paniculate, lateral among leaves at apices of

branchlets, without hooks, occasionally bearing bracteal leaves similar to adult stem leaves (e.g., *Hallé 1680*, P; *Harris & Fay 291*, MO); peduncle 2–6[–7, Léonard, 1949] cm long, slender; branched portion corymbiform, 3–6 × 4–7[–16, Léonard, 1949] cm long, dichotomously branched, axes slender; bracts triangular to ovate, 0.2–1.5 mm long, at apex acute, at base obtuse, marginally denticulate to shortly erose, abaxially eglandular or largest bracts with a gland covering ca. ½ of surface; pedicels 2–6 mm long. *Flowers* all pedicellate; *sepals* 5, oblong to spathulate, rounded at apex, ciliolate at least at apex, straight to a little rounded at base and decurrent on ovary, pale green, 2 or 3 sepals of each flower abaxially with 1 or 2 compressed glands with slender to thickened margins, adaxially apparently without pits, subequal, [2.5–3.5 mm, Léonard, 1949] 4.0–5.0 × 2.0–3.0 mm; *petals* 5, convolute, suborbicular, golden yellow, 2.0–3.0 × 2.0–3.0 mm; *stamens* 10 apparently in 1 whorl; filaments stout, pyramidal, dimorphic, the shorter 0.5–0.7 mm long, the longer 0.8–1.0 mm long; anthers ca. 0.5 mm long, pale orange; *ovary* partially inferior, inferior portion 2.0–3.0 mm long, superior portion ca. 1 mm high; style 1, stout, 1.0–1.5 mm long, red, stigmas 0.5–1.0 mm wide, red. *Fruit* patelliform; nut 4–5 × 7–8 mm, on sides longitudinally shallowly 5-ridged by decurrent margins of accrescent sepals; persistent sepal limbs spreading, coriaceous drying woody, spathulate to obovate or oblong, subequal to unequal, 5–10[–13, Léonard, 1949] × 4–8 mm; pericarp dark brown, coriaceous drying woody; seed ca. 6 mm diam.

Distribution, phenology, and habitat. In inundated and riverine forests at 20–400 m, Central African Republic and Democratic Republic of the Congo to Gabon; collected in flower March, April, and July, in fruit in May and August.

Provisional conservation status. With an EO greater than 20,000 km^2 and existing in the Central African Republic, the Democratic Republic of the Congo, and Gabon: Least Concern; Cheek (2000: 876) also proposed a status of Lower Risk, Least Concern (LR/lc).

This species is distinctive due to its leaves that are most often rather narrowly acuminate, its slender ("delicate," Léonard, 1949) peduncles and inflorescence axes, its solitary style, and its patelliform fruits. It is similar to *Ancistrocladus congolensis*; see additional comments under that species. The petals of *A. ealaensis* are markedly shorter than the sepals. Léonard in his original description gave the sepal length as 2.5–3.5 mm long, but this measurement is significantly shorter than sepals seen by us, and may have been based on buds rather than mature flowers.

The petioles or leaf bases seem to be particularly soft in this species, so that dried specimens typically have a rigid cup of stem tissue enclosing the shrunken leaf base tissue. The structures at the branchlet apices are here interpreted as young leaves that dehisce at their bases and fall off during the drying process; these may be structures interpreted as stipules by Léonard. These are triangular, acuminate, longitudinally folded, and do typically enclose a smaller leaf. No stipule scars are evident here, and each of these structures completely encloses a smaller structure of exactly similar shape, which is here interpreted as another leaf. However, Léonard (1949: 30) observed these plants in the field and described the stipules as "très caduques," which conforms to the behavior of the stipular structures observed on some living plants (pers. obs., CMT, *Ancistrocladus robertsoniorum*, MO greenhouse).

As noted by Léonard (1949), the flowers of this species are frequently attacked by insects that transform them into galls. In fact the majority of collections, unfortunately including the type, bear these galls usually instead of fertile reproductive structures (e.g., *Evrard 1765*, BR). The galls show continuous variation from a globose, clearly galled structure bearing small leaf-like appendages all over it, to an apparently normal large flower with 5 thick large sepals, 5 thick-textured lanceolate petals of similar size to these sepals, about 10 triangular thick filaments also of similar size to these sepals but mostly lacking anthers, and a similar-sized central stylar column. The galls are easily confused with flowers or fruits by those not familiar with this genus.

Selected specimens examined. CENTRAL AFRICAN REPUBLIC. **Sangha Economique:** Ndakan, 2°21′N, 16°09′E, *Harris & Fay 291* (MO). DEMOCRATIC REPUBLIC OF THE CONGO. **Bandundu:** Bokoro, *Jans 879* (BR). **Equateur:** Terr. Bomongo, Ebeka, *Evrard 5950* (BR); environs de Coquilhatville [Mbandaka], *Lebrun 404* (BR). Not located as to province: Mbongo, *Evrard 1765* (BR). GABON. **Moyen-Ogooué:** Makouké, NE of airstrip, 00°29′S, 10°25′E, *Wieringa & Haegens 2633* (WAG). **Ngounie:** Waka Nat. Pk., *Walters et al. 1533* (LBV, MO).

6. Ancistrocladus grandiflorus Cheek, Kew Bull. 55: 878. 2000. TYPE: Cameroon. Southwest Prov.: near Limbe, Mabeta-Moliwe forest, 11 Nov. 1992, *M. Cheek & P. Ndumbe 3915* (holotype, K not seen; isotypes BR not seen, MO not seen, SCA not seen, WAG not seen, YA not seen). Fig. 1, A–E.

Juvenile plants unbranched or sparingly branched saplings to 3 m tall. *Juvenile leaves* oblanceolate, 48.9–79.0 × 10.8–19.3 cm, L/W 4.1–4.8, at apex short- to long-acuminate with acumen to 12 mm long, at base attenuate, drying papyraceous to chartaceous, dull or somewhat shiny especially on abaxial surface, somewhat discolorous, dark often greenish brown adaxially, lighter often yellowish brown abaxially; pits dimorphic, as in adult leaves or large pits sometimes more frequent and apparently filled with wax; midrib plane adaxially, prominent abaxially, terminating in a gland ca. 0.2 mm long; secondary veins 18 to 25 pairs, brochidodromous, with intramarginal vein 3–5 mm from margin; secondary and tertiary venation adaxially and abaxially prominulous; margin thickened, cartilaginous, pale brown. *Adult stems* climbing to 25 m high, main stems to 30 cm diam., with bark dark brown, very rough, slash dark red, bearing some scattered leaves and also lateral branchlets to 27 cm long, these each bearing 1 to several hooks and groups of leaves; *hooks* recurved to spiraling, 12–22 mm diam. *Adult leaves* drying papyraceous to chartaceous, on both surfaces somewhat shiny, in life somewhat discolorous, dark green above, yellow-green below, drying discolorous, dark brown above, lighter brown beneath; pits dimorphic, small pits densely and evenly distributed on abaxial surface, frequent throughout but more concentrated near midrib and margins on adaxial surface, large pits 0.1–0.5 mm diam., circular or broadly elliptic, widely scattered and not present on all leaves, when present mostly located near base on both surfaces; midrib adaxially plane, abaxially prominent, sometimes terminating in a tiny gland; secondary veins prominulous on both surfaces; tertiary veins reticulated, prominulous adaxially, nearly plane to somewhat prominulous abaxially; margins plane to shortly revolute; *stem leaves* with persistence unknown, obovate, 19.6–26.5 × 4.9–7.7 cm, L/W 3.4–4.0, at apex acutely to obtusely acuminate, at base attenuate; secondary veins 10 to 15 pairs, with intramarginal vein situated 2–4 mm from margin; *leaves at branchlet apices* with persistence unknown, obovate, 23.1–42.4 × 8.8–12.2 cm, L/W 2.5–3.7, at apex shortly and obtusely acuminate to rounded, at base short- to long-attenuate; secondary veins 9 to 17[to 19, Cheek, 2000] pairs, with intramarginal vein situated 3–5 mm from margin. *Inflorescence* lax, paniculate, lateral among leaves at apices of branchlets, without hooks or bracteal leaves; peduncle 1.5–4.5 cm long, straight; branched portion corymbiform, [3.5–]5–8 × 2–15 cm, dichotomously branched; bracts oblong-ovate, 1.5–2.4 × 1.0–1.6 mm, at apex acute to obtuse, at base obtuse, abaxially initially eglandular then later developing gland covering up to ¾ of surface; pedicels 3–7[–8] mm long. *Flowers* all pedicellate; *sepals* 4 or 5, oblong to oblong-obovate, rounded and entire to minutely papillate at apex, at base cuneate and shortly decurrent on ovary, green with translucent veins and sometimes tinged red-purple outside, abaxially with 2 to 5 large glands, adaxially with small pits, unequal, the 2 or 3 larger sepals 12.6–14.2 × 5.8–6.2 mm, the 2 smaller sepals [6.5–9.0]9.5–11.3 × [3.0–]4.5–5.0 mm; *petals* 4 or 5, imbricate [contorted], obovate, yellowish white to pale orange [white with pink margins], [9.0–]9.5–12.0 × [4.5–]5.2–6.1 mm; *stamens* 8 or 10 in 2 whorls; filaments stout, the shorter 1.5–2.5 [ca. 4.0] mm long, the longer 2.5–3.3 [ca. 5.0] mm long; anthers 1.1–1.6 mm long; *ovary* ca. ¾ inferior, the inferior portion 4–5 mm long, the superior portion ca. 1 mm long; styles 3, [3.0–3.5]4.5–5.0 mm long, stigmas 0.9–1.1 × 0.7–0.8 mm. *Fruit* not seen.

Distribution, phenology, and habitat. In wet, primary and usually old secondary forests of Cameroon, on both sandy and clay soils, at 60–940 m; collected in flower in November and December.

Provisional conservation status. With an EO of less than 5000 km² and occurring primarily near the well-protected Korup National Park, near Limbe, and in the Rumpi Hills, Cameroon, this taxon is common, though endemic and potentially threatened outside of these areas: Vulnerable (B1ac); based on only four collections from a single forest, Cheek (2000: 879) proposed a status of Critically Endangered (CR A1c+2c, C1+2a).

We have been unable to locate reported isotypes of *Ancistrocladus grandiflorus* at BR, MO, SCA, WAG, and YA. The original description of this species (Cheek, 2000: 879) indicated somewhat smaller sepals and petals, longer filaments, and shorter styles than were observed in the present study, as indicated by measurements in square brackets in the above species description. In fact, the single flowering collection that we have seen from the type locality (*Gereau et al. 5594*) also has somewhat smaller sepals than other flowering specimens examined, within the size range reported by Cheek (2000), but the few flowers present appear slightly immature. More significantly, Cheek (2000: 879, Fig. 1) reported the corolla aestivation of *A. grandiflorus* as contorted, whereas all of the flowering specimens that we have examined have imbricate aestivation; the presence of both convolute and imbricate corolla aestivation within the same species is otherwise known only in *A. congolensis*. Juvenile leaves collected from the type locality (*Gereau et*

al. 5595) are very similar to juvenile leaves collected at higher elevations at other localities (e.g. *Gereau et al. 5560, Letouzey 14589*).

This species is notable for the relatively large size of its flowers within the genus. It is also notable for the number of its sepals and petals, which are frequently 4 rather than 5, and its stamens, often 8 rather than 10. This is the first report of 4-merous flowers in *Ancistrocladus*.

Specimens examined. CAMEROON. **Southwest:** Ndian Div., ca. 8 m [*sic*; km] N of Korup Park Headquarters on Fabe rd. at resettlement site near S bank of tributary to Mana River, 5°04′N, 8°54′E, *R. E. Gereau & P. F. Foster 5485* (MO), *5486* (MO); Manja Village, ca. 1 km ESE of Korup Nat. Park Headquarters in Mundemba, 4°59′N, 8°55′E, *R. E. Gereau & M. Elangwe 5557* (MO, SCA, YA), *5558* (MO, SCA, YA), *R. E. Gereau 5577* (MO, SCA, YA); Meme Div., Mbu Bakundu Village, Mambaba quarter, along rd. above Koba, 5°01′N, 9°20′E, *R. E. Gereau, E. Jato, P. Mambo & I. Iboli 5559* (MO, SCA, YA), *5560* (MO, SCA, YA); Fako Div., baseline of proposed Mabeta-Moliwe For. Res., 2–2.5 km E of Chop Farm–Mabeta rd. & ca. 8 km ESE of Limbe Botanic Garden headquarters, 3°59′N, 9°16′E, *R. E. Gereau, J.-M. Mbani, P. Ndumbe & E. Jato 5594* (MO, SCA, YA), *5595* (MO, SCA, YA); Rumpi Hills, ca. 6 km E of Dikome Balue on foot path to Ifanga Nalende, ca. 300 m E of jct. with trail to Momboriba, 4°55′N, 9°19′E, *R. E. Gereau, F. Namata, E. Jato & E. Sarabe 5630* (MO, SCA, YA), *5634* (MO, SCA, WAG, YA); entre Dikome Balue et Ifanga Nalende, 35 km NNW Kumba, *R. Letouzey 14589* (BR [2], P); forest around Masaka-Batanga, 5°06′N, 9°10′E, *D. W. Thomas & F. Namata* 7745 (MO); Bangang Mbo Council For. Res., ca. 20 km E of Nguti, 1 km E of Mbie River, 5°21′N, 9°35′E, *D. W. Thomas 9992* (MO), *9993* (MO).

7. Ancistrocladus griffithii Planch., Ann. Sci. Nat. Bot., sér. 3, 13: 318. 1849. TYPE: Myanmar [Burma]. Tenasserim, Mergui, s.d., *W. Griffith s.n.* (holotype, K not seen, photo MO!; isotype, P!).

Juvenile plants unknown. *Juvenile leaves* unknown. *Adult stems* arising from extra-axillary buds well below apex of juvenile stem, climbing to 4 m high, to 1 cm diam. [probably becoming larger but no data], with bark purplish brown, smooth to roughened, bearing some scattered leaves and also lateral branchlets to 12 cm long, these bearing groups of leaves; *hooks* not seen. *Adult leaves* drying papyraceous to chartaceous, dull to a little shiny on both surfaces, in life not seen, when dry discolorous, brown to dark brown above, paler brown to yellow-brown below; pits dimorphic, small pits moderately densely distributed to frequent on both surfaces or sometimes only evident on adaxial surface, large pits ca. 0.5 mm diam., circular to oval, few and scattered on adaxial surface; midrib adaxially shallowly sulcate, abaxially prominent, terminating in a tiny gland; secondary veins prominulous on both surfaces; tertiary veins reticulated and prominulous on both surfaces; margins plane to usually revolute; *stem leaves* not seen; *leaves at branchlet apices* with persistence unknown, elliptic, 10.0–30.0 × 1.5–4.3 cm, L/W 4.3–11.5, at apex acute and sometimes abruptly shortly acuminate, at base long-attenuate; secondary veins 11 to 16 pairs, with intramarginal vein situated 1–3 mm from margin. *Inflorescence* lax, paniculate, lateral or apparently terminal among leaves at apices of branchlets, without hooks, occasionally bearing bracteal leaves similar to adult stem leaves (e.g., *Chevalier 31864*, P); peduncle 0.1–10.0 cm long, often flexuous; branched portion corymbiform, ca. 17 × 7 cm, dichotomously branched, axes slender; bracts triangular to lanceolate, ca. 0.8 mm long, at apex acute, at base obtuse to rounded, marginally hyaline and often a little erose, abaxially eglandular or sometimes with a rounded gland covering ½–⅔ of surface; pedicels 1.5–3.0 mm long. *Flowers* all pedicellate, not seen, description based on scale drawings on *Pierre 1791* (P); *sepals* 5, ovate to oblong-obovate, rounded at apex, at base rounded to truncate and shortly decurrent on ovary, abaxially with sparse to numerous small pits, apparently without glands (e.g., *Chevalier 31864*, P), adaxially with small pits, unequal, larger 3 sepals ca. 2.2 × 1.0 mm, smaller 2 sepals ca. 1.9 × 0.9 mm; *petals* 5, apparently imbricate, broadly elliptic, color unknown, ca. 1.7 × 1.1 mm (i.e., slightly shorter than sepals); *stamens* apparently 10 in 2 whorls; filaments stout, pyramidal, dimorphic, the shorter ca. 0.5 mm long, the longer ca. 0.2 mm long; anthers ca. 0.5 mm long; *ovary* fully inferior, size unknown; styles 3, ca. 0.3 mm long, stigmas not seen. *Fruit* turbinate; nut 5–6 × 8–10 mm, on sides longitudinally shallowly 5-ridged by decurrent margins of accrescent sepals; persistent sepal limbs spreading, chartaceous, oblanceolate, subequal, 5–12 × 4–6 mm; pericarp drying dull brown, coriaceous to chartaceous; *seed* obconical, ca. 8 mm diam.

Distribution, phenology, and habitat. To 350 m, habitat not noted, India, Andaman Islands, Burma, Thailand, Cambodia, Vietnam; collected in fruit May and June.

Although it was originally characterized by its relatively long narrow leaves, this species is better characterized and circumscribed by its reproductive characters. It is similar to *Ancistrocladus attenuatus*; for their distinctions see the dicussion there. Also *A. griffithii* can be separated from *A. heyneanus* and *A. tectorius*, which are at least generally sympatric, by its sepals that lack large abaxial

glands, its generally well-developed pedicels, and its inflorescence bracts that are relatively small, clustered at the apices of the axes near the flower buds, apparently caducous at anthesis, and sometimes eglandular. In contrast, these other two species have outer sepals that usually have 1 or 2 abaxial glands, pedicels 0–3 mm long; and bracts that are often well-developed, borne regularly along all the axes, and generally persistent and usually have well-developed abaxial glands.

The name *Ancistrocladus wallichii* has been frequently used for this species (e.g., *Helfer 720*, distributed under this name to at least three institutions; see Dagar & Singh, 1999). However, the type specimens of *A. wallichii* cannot be identified with certainty, and this name is here considered of dubious identity and discussed in that section, below.

Selected specimens examined. CAMBODIA. Bois à Baba, *Godefroy 285 bis* (P). INDIA or MYANMAR [BURMA]. Tenasserim & Andaman Islands, *Helfer 720* (A, C, P [2]). THAILAND. Bangkok, Dom Bang, Supanburi, *Kerr 7006* (BM, C, E, SING). VIETNAM. Mekong River, Kratié, *Chevalier 31864* (P).

8. Ancistrocladus guineensis Oliv., Fl. Trop. Afr. 1: 175. 1868. TYPE: Nigeria. Cross Rivers State: Calabar, 1859–1863, *G. Mann 2234* (holotype, K!; isotypes, GH!, P!).

Ancistrocladus uncinatus Hutch. & Dalziel, Fl. W. Trop. Afr., ed. 1, 1: 196. 1927. Syn. nov. TYPE: Nigeria. Akwa-Ibom State: Eket District, 1912–1913, *P. A. Talbot & Mrs. P. A. Talbot 3108* (holotype, K not seen; isotype, BM!).

Juvenile plants unbranched or sparingly branched saplings to 3 m high. *Juvenile leaves* unknown. *Adult stems* climbing to 15 m high, main stems to 5 cm diam., with bark brown to purple-brown, smooth or with small shallow fissures, bearing some scattered leaves and also lateral branchlets to 25 cm long, these each bearing 1 to several hooks and sometimes a terminal rosette of leaves; *hooks* recurved to spiraling, 9–24 mm diam. *Adult leaves* drying chartaceous to coriaceous, on both surfaces dull to shiny, in life not seen, when dry usually somewhat discolorous, dark brown above, lighter brown below, or sometimes concolorous and gray-tan on both sides; pits dimorphic, small pits sparsely scattered on abaxial surface, sparsely distributed and concentrated near midrib and margins on adaxial surface, large pits 0.3–1.0 mm diam., circular to oval, rare on both surfaces; midrib adaxially plane to shallowly sulcate, abaxially prominent, sometimes terminating in a tiny gland; secondary veins prominulous on both surfaces; tertiary veins reticulated, prominulous adaxially, nearly plane to prominulous abaxially; margins plane to shortly revolute; *stem leaves* with persistence unknown, elliptic to obovate, 5.5–23.1 × 2.6–8.8 cm, L/W 2.0–4.1, at apex obtuse to rounded, at base truncate to cuneate; secondary veins 4 to 11 pairs, with intramarginal vein situated 2–4 mm from margin; *leaves at branchlet apices* with persistence unknown, oblanceolate to obovate, 7.2–33.0 × 3.0–9.4 cm, L/W 2.3–4.8, at apex shortly and acutely or obtusely acuminate to obtuse or rounded, at base attenuate or abruptly narrowly contracted (i.e., pseudopetiolate); secondary veins 7 to 16 pairs, with intramarginal vein situated 2–4 mm from margin. *Inflorescence* lax, paniculate, lateral or subterminal among leaves at apices of branchlets, along peduncle and primary axis occasionally with hooks (e.g., *Jones & Onochie in FHI 16641*, P) or bracteal leaves similar to adult stem leaves (e.g., *Gereau et al. 5603*, MO); peduncle 1.5–8.0 cm long, straight; branched portion corymbiform, 5–15 × 12–20 cm, dichotomously branched; bracts triangular-ovate, 0.8–1.6 × 0.5–1.0 mm, at apex acute to obtuse, at base obtuse, marginally entire, abaxially with a discoid gland covering ca. ½ the surface, occasionally also with 1 or 2 poorly defined pits near base; pedicels 2–5 mm long. *Flowers* all pedicellate; *sepals* 5, oblong to elliptic-oblong, rounded and entire at apex, at base truncate and shortly decurrent on ovary, light green tinged red-purple, abaxially sometimes with 1 to 4 pit-like glands, adaxially with small pits, unequal, larger 3 sepals 3.5–5.1 × 1.4–2.5 mm, shorter 2 sepals 3.2–4.2 × 2.0–2.9 mm; *petals* 5, imbricate, oblong-obovate, pale yellow tinged pink, ca. 8.1 × 3.2 mm; *stamens* 10 in 2 whorls; filaments slender, a little dimorphic, the shorter ca. 4.5 mm long, the longer ca. 5.0 mm long; anthers 0.8–1.0 mm long; *ovary* ca. ¾ inferior, 1–2 mm long; styles 3, ca. 5 mm long, stigmas ca. 0.4 × 0.9 mm. *Fruit* turbinate; nut 5–8 × 3–6 mm, on sides longitudinally shallowly 5-ridged by decurrent margins of accrescent sepals; persistent sepal limbs spreading, papyraceous, dark red, unequal, the larger spathulate to oblanceolate, 28–42 × 13–16 mm, the smaller oblong-spathulate, (5–)12–16 × (4–)5–6 mm; pericarp drying brown, coriaceous; seed not seen.

Distribution, phenology, and habitat. In evergreen vegetation at 80–600 m, including on open roadsides and along rivers, Nigeria to Gabon; collected in flower in March and November, in fruit in February and September.

Provisional conservation status. With an EO greater than 20,000 km² and existing in Cameroon, Gabon, and Nigeria: Least Concern; with far fewer

collections available from a much smaller geographic range, Cheek (2000: 877) proposed a status of Endangered (EN A2c).

The name *Ancistrocladus guineensis* has been widely applied by previous authors to plants belonging to various other species, but in particular to plants treated here as *A. barteri*. Part of the confusion may be due to the specific epithet, which in the modern usage of "Guinea" suggests that this name applies to plants from West Africa. However, the type of *A. guineensis* is from eastern Nigeria, and its range extends from there into Cameroon and Gabon. *Ancistrocladus guineensis* and *A. barteri* are similar in many features, and further study may show these taxa to represent extremes of continuous variation. However, there do appear to be some differences between them, as outlined in the Key to Species above and discussed under *A. barteri*, and they also appear to have disjunct ranges and therefore are provisionally separated here.

Ancistrocladus uncinatus has long been separated from *A. guineensis* based on its smaller leaves, said by previous authors to be variously "6–8 cm long" (Hutchinson & Dalziel, 1927: 196) or "under 8 cm long" (Airy Shaw, 1950: 149). Some leaves on the isotype of *A. uncinatus* (BM!) are as small as this, but others range to significantly larger. When these larger leaf measurements are included in the description of *A. uncinatus*, no differences are evident between this and *A. guineensis*. The isotype of *A. uncinatus* bears an inflorescence fragment with the ultimate axes becoming racemiform, as in *A. guineensis*, and one detached flower. This flower matches those of *A. guineensis* except it is about 20% smaller. However, this flower appears to be very shriveled and its measurements, therefore, are not completely reliable. Although Cheek (2000: 873) reported the petals as tomentose on the outer surface, this condition is not evident on the isotype. The leaves on the type collection of *A. uncinatus* are distinctive in being markedly narrowed toward the base, which gives it at first glance a different general appearance from most collections of *A. guineensis*; however, this distinctive shape is also found on occasional specimens of *A. guineensis* and *A. barteri*, and does not seem to be taxonomically informative.

Selected specimens studied. CAMEROON. **Littoral:** Waouri Div., 40 km E of Douala on hwy. to Edéa, 3°57′N, 10°00′E, *Gereau et al. 5603* (MO, SCA, YA). GABON. **Moyen-Ogooué:** 42 km SE of Lambaréné, border of rivulet of Mamiengue River, 1°S, 10°28′E, *Breteler 5719* (WAG). NIGERIA. **Kwara:** Omo, *Jones & Onochie in F.H.I. 16641* (P). **Ogun:** Ijebu Province, Shasha For. Res., *Richards 3151* (BM, MO).

9. Ancistrocladus hamatus (Vahl) Gilg, Nat. Pflanzenfam. 3(6): 276. 1895. *Wormia hamata* Vahl, Skr. Naturhist-Selsk. 6: 105. 1810. *Ancistrocladus vahlii* Arn., Nova Acta Phys.-Med. Acad. Caes. Leop.-Carol. Nat. Cur. 18: 325. 1836, nom. illeg. *Bigamea hamata* (Vahl) Tiegh., J. Bot. (Morot) 17: 155. 1903. TYPE: Ceylon [Sri Lanka]. Près de Bigamen, s.d., *J. Koenig s.n.* (holotype, C!; isotypes, A!, BM [2]!, C [2]!, L!, P [2]!).

Bigamea thwaitesii Tiegh., J. Bot. (Morot) 17: 155. 1903 [as "*Thwaitesi*"]. *Ancistrocladus thwaitesii* Tiegh., J. Bot. (Morot) 17: 154. 1903 [as "*Thwaitesi*"], nom. invalid. pro syn. TYPE: Ceylon [Sri Lanka]. Without locality, s.d., *G. H. K. Thwaites C.P. 1600* (lectotype, designated here, BM 012417!).

Juvenile plants unknown. *Juvenile leaves* unknown. *Adult stems* climbing with height not noted, to 1 cm diam. [probably becoming larger but no data], with bark purplish brown, smooth to roughened, bearing some scattered leaves and also lateral branchlets to 30 cm long, these each bearing 1 to several hooks and sometimes a terminal rosette of leaves; *hooks* recurved to spiraling, 11–17 mm diam. *Adult leaves* drying papyraceous to chartaceous, on both surfaces shiny, in life not seen, drying discolorous, dark brown above, paler brown or yellow-brown below; pits dimorphic, small pits frequent on both surfaces though usually denser on adaxial surface, large pits 0.4–0.5 mm diam., circular, occasional on adaxial surface; midrib adaxially shallowly sulcate, abaxially prominent, terminating in a tiny gland; secondary veins prominulous on both surfaces; tertiary veins reticulated and prominulous on both surfaces; margins plane to narrowly revolute; *stem leaves* with persistence unknown, elliptic to oblong or oblanceolate, sometimes falcate, 7.1–29.3 × 2.1–7.3 cm, L/W 3.4–5.6, at apex acute to rounded, at base cuneate to acute; secondary veins 10 to 18 pairs; *leaves at branchlet apices* with persistence unknown, elliptic, (8.0–)14.5–33.1 × (2.9–)4.6–8.5 cm, L/W 3.2–6.0, at apex acute to rounded and sometimes abruptly shortly acuminate, at base narrowly cuneate to long-attenuate; secondary veins 15 to 19 pairs, with intramarginal vein situated 1–2 mm from margin. *Inflorescence* lax, paniculate, lateral among leaves at apices of branchlets, occasionally bearing hooks, without bracteal leaves; peduncle 1.2–2.2 cm long, often flexuous; branched portion corymbiform, 7.0–8.5 × 4.5–5.0 cm, dichotomously branched; bracts triangular, 0.7 × 0.4–0.6 mm, at apex acute, at base obtuse, marginally entire to erose at apex, abaxially eglandular; pedicels ca. 2.0 mm long. *Flowers* all shortly pedicellate [not seen; this de-

scription from Thwaites, 1849]; *sepals* 5, elliptic to elliptic-oblong, rounded and entire at apex, at base cuneate to obtuse and decurrent on ovary, color unknown, apparently eglandular abaxially, unequal with apparently 3 larger sepals and 2 smaller sepals; *petals* 5, imbricate, elliptic to suborbicular, color unknown, about equal to longest sepal and longer than other sepals; *stamens* 5, alternate with petals; filaments stout, pyramidal, equal, length unknown; anthers with size unknown; *ovary* fully inferior, ca. 1 mm long; styles 3, size unknown, stigmas not seen. *Fruit* turbinate; nut 20 × 15–19 mm, on sides longitudinally shallowly 5-ridged by decurrent margins of accrescent sepals; persistent sepal limbs spreading, chartaceous to papyraceous, unequal, the 3 larger spathulate, 22–40 × 9–14 mm, the 2 smaller narrowly oblong to spathulate, 8–20 × 5–10 mm; pericarp drying rust brown, coriaceous; *seed* not seen.

Distribution, phenology, and habitat. Moist evergreen forests at 100–150 m, Sri Lanka; collected in flower in April and July, fruiting dates unknown.

Like Harriman (1987), we have seen no collections of this species with flowers adequately preserved for study. The floral morphology of this species is thus still known primarily from the detailed description and figures of Thwaites (1849), which were based apparently on living plants, and Harriman's notes. This species appears from Harriman's figure to have a well-developed disk that surrounds the bases of the three styles, and the typically capitate stigmas appear to be missing from the short linear styles in his figure and his description. Thwaites seems to have considered the receptacular disk to be the style, and the three free linear styles to be the stigmas. Thwaites concentrated most of his descriptive efforts (1849: figs. 6–16) on the ovules, seeds, and embryos, and noted with regard to the general habit of *Ancistrocladus hamatus* that the plant "is very abundant in some of the warmer districts of Ceylon, and owing to its spreading so much by its roots, is a very troublesome weed to the cultivator." Harriman (1987: 2) gave the elevational range of *A. hamatus* as extending up to 2000 m, but the source of his data is not given.

Ramamoorthy (1976) and Harriman (1987) have suggested that *Ancistrocladus hamatus* is synonymous with *A. heyneanus* of continental India. However, these species are clearly distinguished by their stamen number, 5 in *A. hamatus* versus 10 in *A. heyneanus*, and by their fruits, with the nut portion larger (20 × 15–19 mm) in *A. hamatus* and smaller (ca. 5 × 5 mm) in *A. heyneanus*.

The type collection of *Wormia hamata* comprises a number of duplicates that vary markedly in morphology. This collection appears to include samples of the various growth stages of these plants, with these various stages later distributed unevenly among institutions. The isotype at A and one of the isotypes at BM lack hooks and have relatively long narrow leaves that appear to have come from a juvenile plant. Another of the isotypes at BM, one at P, the holotype and isotypes at C, and the isotype at L have fertile hook-bearing branchlets with fruits. The other isotype at P has only one detached leaf, of the form found on the hook-bearing branchlets.

The specimens distributed under the type number of *Bigamea thwaitesii* (*Thwaites 1600*: BM 012417!, BM 012418!, BR [2]!, GH!, HAKS!, L!, P [3]!, SING!, US [2]!) represent a more uniform set. These specimens each have a fertile, hook-bearing branchlet with fruits, except the lectotype at BM has both a hook-bearing branchlet and a robust, perhaps juvenile stem with markedly larger leaves. Tieghem (1903) treated the *Ancistrocladus* plants of Sri Lanka as a distinct endemic genus, *Bigamea*, based on their 5 rather than 10 stamens, and regarded *Bigamea* as comprising two species, the previously described *B. hamata* and his new species *B. thwaitesii*. Tieghem (1903) actually used two different names in this article for his new species, *A. thwaitesii* (p. 154) and *B. thwaitesii* (p. 155), but he did state clearly that *B. thwaitesii* was the name he accepted, thus this name must be considered the one that is validly published. Tieghem separated his two Sri Lankan species based on leaf dimensions, 20 × 4 cm in *B. thwaitesii* versus 8 × 2.5 cm in *B. hamata*, and also by the leaf blades being less coriaceous with flat margins in *B. thwaitesii* versus coriaceous with revolute margins in *B. hamata*. However, Thwaites regarded the Sri Lankan plants as all belonging to one species, so his specimens were all distributed under the same number. No specimens have been found that were annotated as *B. thwaitesii* by Tieghem, and his nomenclatural work does not always conform to modern standards so interpretation of his intent is sometimes difficult. Of the 13 duplicates of *Thwaites C.P. 1600* that were studied, only BM 012417 matches Tieghem's description of *Bigamea thwaitesii*. Thus we have selected this specimen as the lectotype and we exclude the remaining duplicates listed above from this typification; another duplicate reported to be at K has not been seen.

Selected specimens examined. SRI LANKA. **Western:** Kulatara Dist., Morapitiya, *L. H. Cramer 4179* (E, US); Morapitiya, *A. J. Kostermans 24676* (E, L [2], P, US); Ratnapura Dist., Gilimale Forest, *L. Bernardi 16073* (US).

10. Ancistrocladus heyneanus Wall. ex J. Graham, Cat. Pl. Bombay 28. 1839. TYPE: Locality unknown but presumably India, s.d., *Herb. Heyne s.n. in Wallich Numer. List 7262* (holotype, K!; isotypes, BM!, C!, K-WALL!).

Juvenile plants unknown. *Juvenile leaves* unknown. *Adult stems* climbing with height not noted, to 1 cm diam. [probably becoming larger but no data], not twining, sparingly branched, with bark purplish brown, smooth to markedly roughened, bearing a few scattered leaves and lateral branches to 25 cm long, these each bearing 1 to several hooks and usually a cluster of leaves; *hooks* recurved to spiraling, 10–18 mm diam. *Adult leaves* drying chartaceous to subcoriaceous, on both surfaces somewhat shiny to matte, in life concolorous (pers. obs., CMT, MO greenhouse), when dry concolorous or a little discolorous, brown or gray to brownish green or grayish green; pits dimorphic, small pits frequent to dense on both surfaces, large pits ca. 0.4 mm diam., round to elliptic, present on only some leaves, 2 to 6 per leaf on abaxial surface; midrib adaxially plane to a little prominulous, abaxially prominulous to prominent, terminating in a tiny gland; secondary veins thinly prominulous on both surfaces; tertiary veins finely reticulated and narrowly prominulous on both surfaces; margins plane; *stem leaves* with persistence unknown, obovate or oblanceolate, 6.2–11.1 × 2.4–4.8 cm, L/W 2.0–3.2, at apex rounded, at base truncate to broadly attenuate; secondary veins poorly defined, 8 to 10 pairs, intramarginal vein not evident; *leaves at branchlet apices* with persistence unknown, narrowly oblanceolate to elliptic-oblong, 9.2–49.5 × 2.9–11.0 cm, L/W 2.1–6.3, at apex acute to shortly acuminate or occasionally obtuse, at base narrowly cuneate to acute; secondary veins 9 to 12 pairs, with intramarginal vein situated 2–4 mm from margin. *Inflorescence* lax, paniculate, lateral, subterminal, or apparently terminal among leaves at apices of branchlets, without hooks, rarely bearing bracteal leaves similar to adult stem leaves; peduncle 0.6–4.0 cm long, often rather stout; branched portion corymbiform, 2.5–15.0 × 4–25 cm, dichotomously branched 1 or 2 times, subsequently racemiform; bracts ovate to elliptic, 1.5–3.0 mm long, at apex obtuse to acute, at base obtuse, abaxially with a round gland occupying ½–⅔ of surface; pedicels 0–1 mm long. *Flowers* sessile to pedicellate; *sepals* 5, elliptic-oblong, rounded at apex, at base truncate and shortly decurrent on ovary, color unknown, 1 to 3 sepals abaxially with 2 or 3 elliptic glands ca. 0.2 mm diam., adaxially smooth or with moderately to densely distributed small pits, equal or subequal, 6.0–6.5 × 3.0–3.5 mm; *petals* 5, convolute, elliptic to obovate, color unknown, 6.0–7.0 × 4.0–4.5 mm; *stamens* 10 in 1 whorl; filaments stout, pyramidal, apparently subequal, 1.0–1.5 mm long; anthers ca. 0.5 mm long; *ovary* fully inferior, 2–3 mm long; styles and stigmas not seen. *Fruit* turbinate; nut ca. 5 × 5 mm, on sides longitudinally shallowly 4- or 5-ridged by decurrent margins of accrescent sepals; persistent sepal limbs spreading, chartaceous to papyraceous, unequal, larger 3 sepals oblanceolate, 25–40 × 12–17 mm, smaller 2 sepals narrowly oblong to spathulate or oblanceolate, 19–26 × 5–7 mm; pericarp drying light to cinnamon brown, coriaceous; *seed* not seen.

Distribution, phenology, and habitat. Seasonal to evergreen forests, low elevations in the Western Ghats mountains of southwestern India; collected in flower in January, in fruit in March and April.

Das (1993) reported this species from Karnataka, Kerala, Maharashtra, and Tamil Nadu states, India, without citation of voucher specimens; we have seen specimens only from Karnataka, but we have no reason to doubt his report.

We have seen no well-preserved flowers of this species. Wight (1853: t. 1987–1988) depicted the flowers of this species as similar in morphology to most other species of *Ancistrocladus*, and as having sepals about equal in length to the petals and the longer stamen filaments about ⅓ as long as the petals. Das (1993) described this species as having filaments 6–9 mm long, which implies that the petals, at three times the length of the longer filaments, are ca. 27 mm long, which does not agree with any other descriptions of this species, nor with his own description of the petals as 6–8 mm long. Ramamoorthy (1976) described *A. heyneanus* as having nine stamens with four reduced to staminodes, but this appears to be a misinterpretation of *Ancistrocladus*'s unequal but all fertile stamens.

Ancistrocladus heyneanus is very similar to *A. tectorius* of southeast Asia. These are distinguished by the lengths of their petals, 6–7 mm long in *A. heyneanus* versus 3.2–5.5 mm long in *A. tectorius*, and by their disjunct geographic ranges. We disagree with the suggestion by Ramamoorthy (1976) and Harriman (1987) that *A. heyneanus* may be conspecific with *A. hamatus* of Sri Lanka; the distinctions between these two species are outlined in the discussion of *A. hamatus*.

Representative specimens studied. INDIA. **Karnataka:** Bisle Ghat, Hassan Dist., Mysore, *Ramamoorthy & Gandhi 2723* (E, MO, US); rd. from Kumta to Sirsi, N Kanara, Bombay Presidency, *Fernandes 175* (A).

11. Ancistrocladus korupensis D. W. Thomas &

Gereau, Novon 3: 494. 1993. TYPE: Cameroon. Southwest Prov.: Ndian Div., 0.6 km E of confluence of Mededibe (Moliba) & Ndian (Mana) Rivers, 5°02′N, 8°53′E, 90 m, 4 Mar. 1993, *R. E. Gereau, D. W. Thomas, F. Namata & E. Jato 5180* (holotype, MO4568407!; isotypes, K!, P!, SCA!, YA!).

Juvenile plants unbranched or sparingly branched saplings to 4 m tall, lacking hooked branchlets. *Juvenile leaves* numerous in terminal rosettes, long-lived, oblanceolate, 38.8–75.1 × 9.5–13.8 cm, L/W 3.5–5.4, at apex acute to acuminate, at base attenuate, drying papyraceous to chartaceous, dull to shiny on both surfaces; pits dimorphic, similar to those of adult leaves; midrib adaxially shallowly sulcate, abaxially prominent, terminating in a tiny gland; secondary veins 23 to 35 pairs; secondary and tertiary venation adaxially and abaxially prominulous; margins plane to thinly revolute. *Adult stems* arising from extra-axillary buds well below apex of juvenile stem, climbing to 20 m high, main stems to 14 cm diam., not twining, sparingly branched, with bark purplish brown, smooth to roughened, bearing scattered leaves and lateral branchlets to 50 cm long, these each bearing 1 to several hooks and sometimes a terminal rosette of leaves; *hooks* recurved to spiraling, 9–19 mm diam. *Adult leaves* drying papyraceous to chartaceous, on both surfaces shiny, in life a little discolorous, green above, yellow-green below, when dry discolorous, dark green above, yellow-green below; pits dimorphic, small pits sparse to frequent on both surfaces though usually denser on adaxial surface, large pits 0.4–0.6 mm diam., circular or broadly elliptic, scattered on abaxial surface, scattered usually near base on adaxial surface; midrib adaxially nearly plane to shallowly sulcate, abaxially prominent, terminating in a tiny gland; secondary veins prominulous on both surfaces; tertiary veins reticulated and prominulous on both surfaces; margins narrowly to markedly revolute; *stem leaves* apparently long-lived, elliptic to oblong or oblanceolate, 12–57 × 5.0–12.8 cm, L/W 3.5–4.2, at apex acute to rounded, at base cuneate to acute; secondary veins 7 to 20 pairs; *leaves at branchlet apices* persisting up to 3 years, oblanceolate, (8.0–)14.5–34.2 × (2.9–)4.6–11.0 cm, L/W 2.9–4.2, at apex acute to rounded and sometimes abruptly shortly acuminate, at base narrowly cuneate to long-attenuate; secondary veins 8 to 18 pairs, with intramarginal vein situated 2–4 mm from margin. *Inflorescence* lax, paniculate, lateral among leaves at apices of branchlets, occasionally bearing hooks (e.g., *Gereau et al. 5532*, MO), without bracteal leaves; peduncle (4.0–)5.5–13.0 cm long, often flexuous; branched portion corymbiform, 7–16 × 12–20 cm, dichotomously branched; bracts triangular to narrowly ovate, 0.5–1.0 × 0.2–0.4 mm, at apex acute to obtuse, at base obtuse, abaxially eglandular; pedicels 6–9 mm long. *Flowers* pedicellate, rarely (e.g., *Gereau & Thomas 5204*, MO) borne singly on hook-bearing branches from sapling; *sepals* 5, suborbicular to elliptic-oblong, rounded and ciliolate at apex, at base rounded to truncate and shortly decurrent on ovary, pale yellow-green to greenish white with slender brown to translucent veins, abaxially apparently eglandular, adaxially with small pits, unequal, larger 3 sepals 5.0–6.0 × 3.0–4.0 mm, smaller 2 sepals 2.5–3.5 × 2.0–3.5 mm; *petals* 5, convolute, suborbicular, pale yellow to pale rose-pink, 2.0–3.0 × 2.0–2.9 mm; *stamens* 10 in 2 whorls; filaments stout, dimorphic, the shorter 0.5–0.7 mm long, the longer 0.8–1.3 mm long; anthers 0.5–0.8 mm long; *ovary* fully inferior, 1–3 mm long; styles 3, ca. 2 mm long, stigmas ca. 0.5 mm long. *Fruit* turbinate; nut 10 × 10–12 mm, on sides longitudinally shallowly 5-ridged by decurrent margins of accrescent sepals; persistent sepal limbs spreading, chartaceous to papyraceous, unequal, larger 3 sepals spathulate to oblanceolate, 34–48 × 13–21 mm, smaller 2 sepals narrowly oblong to spathulate, 11–28 × 4–11 mm; pericarp drying dull brown, coriaceous; *seed* obconical, ca. 8 mm diam.

Distribution, phenology, and habitat. Moist evergreen forests at 50–360 m, southeast Nigeria to westernmost Cameroon; collected in flower in February and November, in fruit in March and December.

Provisional conservation status. With an EO of less than 5000 km² and occurring primarily within the well-protected Korup National Park, Cameroon, and neighboring Oban Hills of Nigeria, this taxon is common, though endemic and potentially threatened outside of these areas: Vulnerable (B1ac); Cheek (2000: 876) proposed a status of Lower Risk, but Conservation Dependent (LR/cd).

Thomas and Gereau (1993) provided detailed information about the physical environment, ecology, and phytochemistry of this species. This species was initially misidentified as *Ancistrocladus abbreviatus*, and Bringmann et al. (1990) and Manfredi et al. (1991) reported studying *A. abbreviatus*, but actually studied the alkaloids of *A. korupensis*, which had not yet been described when they published their work (Foster & Sork, 1997). Boyd et al. (1994) and Bringmann and Pokorny (1995) also investigated the chemistry of this species. Foster and Sork

(1997) studied in detail the population and genetic structure and alkaloid content of this species in Korup National Park in Cameroon. Label data for *D. W. Thomas 9971* (MO) report flowers of *A. korupensis* opening at night and with a faint aromatic odor; this is the only report of floral biology for any species of the genus.

Selected specimens examined. CAMEROON. **Southwest:** Ndian Div., Korup Nat. Park, Science Camp 1, 5°01′N, 8°48′E, *Gereau et al. 5175* (MO); Chimpanzee Camp, 9.2 km by trail NNW of Mana River suspension bridge, 5°04′N, 8°52′E, *Gereau et al. 5532* (MO); Mundemba, W of Ekendu Kundu road on hunting trail, 5°01′N, 8°53′E, *Gereau et al. 5517* (MO), *5661* (MO). NIGERIA. **Cross River:** Oban, *Talbot & Talbot 1726* (BM).

12. Ancistrocladus letestui Pellegr., Bull. Soc. Bot. France 98: 18. 1951. TYPE: Gabon. Estuaire Prov.: región de Lastoursville, región de Monts Iboundji, 27 Dec. 1930, *G. M. P. C. Le Testu 8627* (holotype, P!; isotypes, BM!, BR!, EA!).

Juvenile plants branched saplings to 2 m tall, lacking hooked branchlets; stems usually with small epidermal protuberances near apex. *Juvenile leaves* numerous, crowded near apex of sapling branches, linear-lanceolate, 29.0–35.5 × 1.4–1.6 cm, L/W 20.7–25.4, at apex caudate-attenuate then narrowly rounded at tip, at base long-attenuate with blade tissue ultimately very narrow, drying papyraceous; pits monomorphic, small, scattered on abaxial surface, on adaxial surface few and scattered along midrib, margins, and apex; midrib adaxially narrow and very shallowly sulcate, abaxially prominent, on some leaves terminating in a gland ca. 0.2 mm diam.; secondary veins ca. 40 pairs, brochidodromous; secondary and tertiary venation adaxially prominulous and poorly differentiated from each other, abaxially secondary prominulous and tertiary venation plane to slightly sunken; margins plane to thinly revolute. *Adult stems* climbing to 30 m high, to 5 cm diam., not twining, with bark gray, with shallow longitudinal fissures, bearing some scattered leaves and lateral branchlets to 30 cm long, lateral branchlets each bearing 1 to several hooks and sometimes a terminal cluster of leaves, main stems and lateral branchlets smooth or sometimes with small epidermal protuberances similar to those on saplings; *hooks* recurved to spiraling, 7–16 mm diam. *Adult leaves* drying chartaceous, on both surfaces dull or somewhat shiny, in life not seen, drying discolorous, dark brown above, somewhat lighter brown beneath; pits dimorphic, small pits sparse to frequent though scattered on abaxial surface, sparse and concentrated along margins on adaxial surface, large pits (0.5–)2.0–4.0 × 0.5–1.0 mm, oblong or sometimes circular, 1 to 3 on each surface; midrib adaxially narrow and plane to shallowly sulcate, abaxially prominent, sometimes terminating in a tiny gland; secondary veins prominulous on both surfaces; tertiary veins reticulated and prominulous on both surfaces; margins plane to thinly revolute; *stem leaves* with persistence unknown, narrowly oblanceolate to oblanceolate, 4.0–42.9 × 1.1–5.1 cm, L/W 3.0–17.2, at apex acute to rounded, at base truncate to long-attenuate; secondary veins 8 to 33 pairs; *leaves at branchlet apices* with persistence unknown, narrowly oblanceolate to elliptic-oblanceolate, 7.5–32.4 × 1.0–6.7 cm, L/W 3.5–15.5, at apex rounded or obtuse to attenuate then narrowly rounded or subacute, at base long-attenuate; secondary veins 8 to 23 pairs, with intramarginal vein situated 1–4 mm from margin. *Inflorescence* lax, paniculate, lateral or subterminal among leaves at apices of branchlets, without hooks, occasionally bearing bracteal leaves similar to adult stem leaves (e.g., *Le Testu 8627*, P); peduncle 2.2–6.2 cm long, sometimes curved; branched portion corymbiform, 6–13 × 12–23 cm, dichotomously branched; bracts at early anthesis lanceolate to triangular-oblanceolate, 1.0–1.9 × 0.6–0.8 mm, at apex acute to obtuse and fimbriate, at base spathulate to acute, abaxially with a discoid gland occupying ½–⅔ of the surface, by late anthesis bracts growing to 3.0–3.5 mm long and becoming cochleate to clavate by expansion of gland and incurving of enlarged apex; pedicels 4–9 mm long. *Flowers* all pedicellate; *sepals* 5, oblong, rounded and entire at apex, at base truncate and shortly decurrent on ovary, red-orange, abaxially often with 1 or 2 raised glands, adaxially with a few small pits, subequal, 2.0–3.0 × 1.0–2.1 mm; *petals* 5, convolute, suborbicular, cream, ca. 2.5 × 2.5 mm; *stamens* 10 in 2 whorls; filaments stout, the shorter ca. 0.3 mm long, the longer ca. 0.7 mm long; anthers ca. 0.4 mm long; *ovary* partially inferior, 1–3 mm long; styles (2 or) 3, ca. 0.9 mm long, stigmas ca. 0.3 mm long. *Fruit* turbinate; nut ca. 6 × 7 mm, on sides longitudinally shallowly 5-ridged; persistent sepal limbs spreading, chartaceous, unequal, larger 3 sepals oblanceolate, 34 × 11–12 mm, smaller 2 sepals oblanceolate to spathulate, 21 × 8–10 mm; perianth drying brown, chartaceous; *seed* not seen.

Distribution, phenology, and habitat. River margins and hills, 125–950 m, Nigeria to Gabon and Republic of the Congo; collected in flower in

June and December (fruiting collections without month).

Provisional conservation status. With an EO greater than 20,000 km² and existing in Nigeria, Cameroon, Gabon, and the Republic of the Congo: Least Concern; with far fewer collections available, Cheek (2000: 875) proposed a status of Data Deficient (DD).

The large pits on the leaves of *Ancistrocladus letestui* are usually oblong and larger in size than in other species of *Ancistrocladus* and apparently are distinctive for this species when they are present. The mature inflorescence bracts also appear to be distinctive for this species: on young inflorescences they have a form similar to the bracts of several other species, ovate with a central abaxial gland, but as the flower buds develop they become elongated below the abaxial gland, which enlarges markedly giving the bracts a spathulate shape with a cucullate apex. These distinctive bracts persist through the fruiting stage (e.g., *Hallé 2648*, P). Also frequently distinctive in *A. letestui* is the bark of the branchlets, which is often ornamented with small protuberances formed from obtuse cylindrical multicellular extensions of the epidermis; however, these structures are not found on all specimens of this species. A number of specimens of *A. letestui* also are distinctive in having relatively very narrow leaves, but leaf shape varies markedly within the species and does not alone distinguish *A. letestui* (e.g., *Hallé 3955*, P, with the full range of leaf forms, the distinctive bracts, and the distinctive branchlet protuberances).

Selected specimens. CAMEROON. **South:** Océan Div., forested summit of Mont Ngoyang, ca. 5 km W of Ngoyang village, this ca. 12 km N of Lolodorf on rd. to Eséka, 3°21′N, 10°43′E, *Gereau et al. 5616* (MO), *5622* (MO). GABON. **Estuaire:** Monts de Cristal, near Kinguélé Dam, 0°40′N, 10°23′E, *McPherson 15140* (MO). **Ogooué Ivindo:** Makokou, *Hallé 2648* (P); Belinga Mountains, Crête de Babiel, *Hallé 3955* (P [3]). NIGERIA. **Cross River:** Awi Dist., Awi For. Res., *Gbile & Daramola 77/80* (FHI-93472). REPUBLIC OF THE CONGO. **Sangha:** near Poumba-Ekok, 10 km S of Belle Vue on rd. from Souanké to Garabinzam, 2°00′N, 13°55′E, *Thomas 9003* (MO).

13. Ancistrocladus likoko J. Léonard, Bull. Soc. Roy. Bot. Belgique 82: 34. 1949. TYPE: Democratic Republic of the Congo. Orientale Prov.: Forestier Central, rivière Boamba, environs de Yangambi, July 1948, *J. Léonard 1850* (holotype, BR!; isotypes, BR [2]!, P!, YBI not seen).

Juvenile plants unknown. *Juvenile leaves* unknown. *Adult stems* climbing to 12 m high, main stems to 5 cm diam., with bark purplish gray to brown, smooth to roughened, bearing lateral branchlets to 15 cm long, these each bearing 1 to several hooks and a cluster of leaves; *hooks* recurved to spiraling, 10–15(–25) mm diam. *Adult leaves* drying coriaceous to chartaceous, on both surfaces shiny, in life not seen, drying discolorous, darker adaxially, paler abaxially; pits dimorphic, small pits frequent on both surfaces though usually denser on adaxial surface, large pits 0.3–0.4 mm diam., circular or broadly elliptic, occasional on both surfaces; midrib adaxially plane to shallowly sulcate, abaxially prominent, sometimes terminating in a tiny gland; secondary veins prominulous on both surfaces; tertiary veins reticulated and prominulous on both surfaces; margins revolute to strongly so; *stem leaves* with persistence unknown, elliptic-obovate, 5.0–8.1 × 2.1–3.5 cm, L/W 2.3–2.4, at apex acuminate to rounded, at base cuneate to acute; secondary veins 7 or 8 pairs, with intramarginal vein situated 1–3 mm from margin; *leaves at branchlet apices* with persistence unknown, obovate, 8.0–40.0(–50.0) × 3.0–13.0 cm, L/W 2.1–3.5, at apex obtuse to rounded and sometimes abruptly shortly acuminate and a little falcate with acumen 1–2(–10) mm long, at base narrowly cuneate to long-attenuate; secondary veins 9 to 15 pairs, with intramarginal vein situated 1–3 mm from margin. *Inflorescence* lax, paniculate, lateral among leaves at apices of branchlets, occasionally bearing hooks, without bracteal leaves; peduncle 3.5–11.0 cm long; branched portion corymbiform, 6–24 × 4–15 cm, dichotomously branched; bracts ovate or depressed-ovate, 1.0–1.5 × 1.0–2.0 mm, at apex acute and hyaline, at base obtuse, abaxially with a discoid gland covering ⅔–¾ of surface, with 1 or usually 2 pits on each side; pedicels 1–4 mm long. *Flowers* all pedicellate; *sepals* 5, elliptic-oblong, at apex cucullate and rounded, at base rounded, thickened, and decurrent on ovary, marginally crenulate, white-green when young becoming brownish, abaxially with 2 to 4 elliptical glands, somewhat unequal, 5.0–9.0 × 3.0–6.0 mm; *petals* 5, convolute, suborbicular, cream-yellow, 3.0–4.0 × 3.0–4.0 mm; *stamens* 10 in 1 whorl; filaments pyramidal, white, dimorphic, the shorter ca. 0.4 mm long, the longer ca. 1.2 mm long; anthers ca. 1.0 mm long, yellow; *ovary* partially inferior, ca. 1.0 mm long; style 1, 2.0–3.0 mm long, stigmas ca. 0.3 mm long. *Fruit* turbinate; nut 10–18 × 12–18 mm, on sides deeply canaliculate, 10-ridged by strongly thickened decurrent margins of accrescent sepals; persistent sepal limbs spreading, coriaceous to woody, spathulate, generally equal, 8–12 × 4–7 mm; pericarp drying dull brown, coriaceous; *seed* obconic, 7 × 9–10 mm.

Distribution, phenology, and habitat. Heliophiles found along rivers and in swamp forests at 430–470 m (this elevational range is based on two collections with data; the actual range is probably wider), Democratic Republic of the Congo; collected in flower and fruit throughout the year except December.

Provisional conservation status. With an EO greater than 20,000 km² in the Democratic Republic of the Congo: Least Concern; Cheek (2000: 876) also proposed a status of Lower Risk, Least Concern (LR/lc).

The fruits float and are water-dispersed (Léonard, 1949). Léonard (1982) noted that the fruits are frequently transformed into galls with dimensions of 1.3–2.0 × 2.2–2.5 cm. The flowers of this species are similar to those of *Ancistrocladus ealaensis*; these species can be distinguished by the size of the nut body, 10–18 × 12–18 mm in *A. likoko* versus 4–5 × 7–8 mm in *A. ealaensis*. Gereau (1997) attempted to correct the specific epithet to "likokoi," but Léonard (pers. comm.) has confirmed that he intended the epithet to stand as a noun in apposition so it is here restored to its original orthography.

Selected specimens examined. DEMOCRATIC REPUBLIC OF THE CONGO. **Equateur:** Ikaku-Busira, *J. Ghesquière 2780* (BR, P, WAG); Eala, *J. Leemans 240* (BR). **Orientale:** Yangambi, Isangi Territory, *Mullenders 2423* (BR, WAG); Tshopo zona, Basoko, *F. Szafranski 1287* (BR).

14. Ancistrocladus robertsoniorum J. Léonard, Bull. Jard. Bot. Belg. 54: 466. 1984. TYPE: Kenya. Coast Prov.: Kwale Dist., Buda Forest, 60 m, 7 Sep. 1983, *Mrs. S. A. Robertson 3687* (holotype, BR!; isotype, BR!, K not seen).

Juvenile plants unbranched or sparingly branched saplings to 4 m high, lacking hooked branches until late in development. *Juvenile leaves* somewhat crowded near apex of stem but not borne in rosettes, oblanceolate, 43.5–55.0 × 9.1–10.3 cm, L/W 4.7–5.3, at apex obtuse to acute, at base attenuate, drying chartaceous to subcoriaceous; pits dimorphic, similar to those of adult leaves; midrib adaxially slightly to strongly raised, abaxially prominent, terminal gland not found; secondary veins 19 to 27 pairs; secondary and tertiary venation adaxially prominulous, abaxially more strongly so; margins plane to thinly revolute. *Adult stems* climbing to 15 m high, to 3.5 cm diam., with bark dark brown, roughened, bearing scattered leaves and lateral branchlets to 25 cm long, these each bearing 1 to several hooks and sometimes a terminal cluster of leaves; *hooks* recurved to spiraled, 9–17 mm diam. *Adult leaves* drying chartaceous, on both surfaces matte to rather shiny, in life (pers. obs., CMT, MO greenhouse) and when dry discolorous, dark green above, yellow-green below; pits dimorphic, small pits moderately to densely distributed on both surfaces though sometimes denser on the adaxial surface, large pits circular, 0.2–0.4 mm diam., scattered on abaxial surface; midrib adaxially plane to distinctly raised, abaxially prominent, terminating in a tiny gland; secondary veins prominulous on both surfaces; tertiary veins reticulated on both surfaces; margins thinly revolute; *stem leaves* with persistence unknown, narrowly obovate-elliptic, 18.4–50.0 × 5.3–10.2 cm, L/W 3.3–4.5, at apex obtuse, at base attenuate; secondary veins 14 to 24 pairs, with intramarginal vein not evident; *leaves at branchlet apices* with persistence unknown, obovate-elliptic, narrowly elliptic, or oblanceolate, 6.5–30.0 × 2.0–7.5 cm, L/W 3.0–4.4, at apex acute to obtuse and sometimes very shortly acuminate or rounded to shortly emarginate, at base attenuate to acute and tapered then sometimes shortly abruptly rounded; secondary veins 10 to 25 pairs, with intramarginal vein 0–1 mm from margin. *Inflorescence* lax, paniculate, lateral among leaves at apices of branchlets, without hooks or bracteal leaves; peduncle 1.0–4.5 cm long; branched portion corymbiform, 4–11 × 5–15 cm, dichotomously branched; bracts ovate, 1.0–1.7 × 1.0 mm, at apex acute and fimbriate, at base obtuse, abaxially eglandular; pedicels 5–12 mm long. *Flowers* all pedicellate; *sepals* 5, elliptic to elliptic-oblong, at apex and base rounded, green sometimes tinged red near apex, marginally entire to sparsely ciliate, abaxially eglandular, sometimes both surfaces with small pits, subequal, 4.0–7.0 × 3.0–4.0 mm; *petals* 5, convolute (e.g., *Luke 3343*, MO; called "imbricate" by Léonard, 1986), obovate, greenish cream or yellow to buff or white sometimes tinged with pink, 5.0–7.0 × 3.4–3.6 mm; *stamens* 10 in 2 whorls [10 to 15 arranged in 1 or 2 whorls, Léonard, 1986]; filaments rather stout, dimorphic, the shorter 1.0–1.2 mm long, the longer 1.5–2.0 mm long; anthers ca. 0.7 mm long; *ovary* partially inferior, ca. 1.5 mm long; styles 3, ca. 3 mm long, stigmas ca. 0.5 mm long. *Fruit* turbinate; nut 5–8 × 5–6 mm, on sides longitudinally shallowly 5-ridged by decurrent margins of accrescent sepals; persistent sepal limbs spreading, chartaceous, elliptic-oblanceolate to spathulate, unequal, continuously grading in size, the largest 23–50 × 5–15 mm, the smallest 10–20 × 4–8 mm; pericarp drying chestnut brown; *seed* obconical, 3–4 × 4–5 mm, whitened.

Distribution, phenology, and habitat. Moist evergreen coastal forest at 25–300 m, southeastern Kenya; collected in flower and fruit in November.

Provisional conservation status. With an EO of less than 5000 km² and with a distribution limited to three sites in coastal Kenya, which support vigorous populations but are under threat from mining and illegal logging, and already listed as potentially threatened (Gereau & Luke, 2003): Endangered (B1ab); Cheek (2000: 878) reported an assessment of Critically Endangered.

Léonard (1984, 1986) noted that unlike other *Ancistrocladus* species, the stamen number of this species varies and sometimes ranges to as many as 15 stamens, with the number of whorls of filaments also variable; we have not confirmed either of these observations.

Selected specimens examined. KENYA. **Coast:** Buda Forest, 4°27′S, 39°24′E, *Polhill & Robertson 4786* (BR [4], EA, MO, WAG); Buda Mafisini Forest, 8 mi. WSW of Gazi, *Drummond & Hemsley 3936* (EA, K not seen photo EA!, WAG); Kwale Dist., Gongoni For. Res., *Luke 3343* (MO), *Robertson & Luke 5972* (EA, MO); ca. 4.6 km WNW of Mombasa-Lunga Lunga rd. & 14 km WSW of Diani Beach on old logging track in N-central part of reserve, 4°24′S, 39°28′E, *Gereau & Lumumbah 5474* (MO), *5475* (MO), *5477* (MO).

15. Ancistrocladus tanzaniensis Cheek & Frim., Kew Bull. 55: 207. 2000. TYPE: Tanzania. Iringa Region: Iringa Dist. [Iringa Rural Dist.], Uzungwa [Udzungwa] Scarp Forest Reserve, 8°21′S, 35°58′E, 1100 m, 15 Dec. 1997, *C. Frimodt-Møller, H. Ndangalasi & Jøker s.n. in TZ-537* (holotype, K not seen; isotypes, C not seen, DSM!).

Juvenile plants unknown. *Juvenile leaves* unknown. *Adult stems* climbing to 25 m high, to 13 mm diam. [possibly becoming larger but no data], not twining, sparingly branched, with bark purplish brown, smooth to roughened, bearing scattered leaves and lateral branchlets to 30 cm long, these each bearing 1 to several hooks and usually a terminal cluster of leaves; *hooks* recurved to shortly spiraling, 5–15 mm diam. *Adult leaves* drying chartaceous, on both surfaces rather shiny, in life not seen though reportedly pink when flushing, drying discolorous, dark green above, yellow-green below; pits dimorphic, small pits sparse on both surfaces and distributed largely along midrib and near margins and apices, large pits 0.2–0.8 mm diam., circular, scattered on both surfaces; midrib adaxially plane or shallowly sulcate, abaxially prominent, terminating in a tiny gland; secondary veins prominulous on both surfaces; tertiary veins reticulated and prominulous on both surfaces; margins revolute to thinly so; *stem leaves* with persistence unknown, oblanceolate, 18.0–52.5 × 7.4–8.7 cm, L/W 2.4–6.0, at apex obtuse, at base tapered and abruptly shortly rounded; secondary veins 10 to 19 pairs, with intramarginal vein not evident; *leaves at branchlet apices* with persistence unknown, oblanceolate to narrowly so, 9.0–38.5 × 2.5–8.5 cm, L/W 4.0–5.8, at apex obtuse to rounded, at base cuneate to acute and shortly abruptly rounded; secondary veins 10 to 18 pairs, with intramarginal vein situated 1–3 mm from margin. *Inflorescence* lax, paniculate, lateral among leaves at apices of branchlets, sometimes bearing hooks (e.g., *C. Frimodt-Møller et al. s.n. in TZ-537*, DSM), sometimes with bracteal leaves resembling reduced adult stem leaves (e.g., *Mbago 1803*, MO); peduncle 1.1–3.5 cm long; branched portion corymbiform, 3.5–8.0 × 6–11 cm, dichotomously branched; bracts triangular to elliptic, 1.1–1.8 mm long, at apex acute to obtuse, entire or sometimes fimbriate, at base obtuse, abaxially with a discoid gland occupying ⅓–⅔ of surface; pedicels 3.0–8.5 mm long. *Flowers* all pedicellate, seen in bud only; *sepals* 5(?), elliptic to suborbicular, rounded at apex, at base cuneate and shortly decurrent on ovary, yellow, apparently a little unequal, 2.5–3.5 mm long, ciliolate at apex, perhaps with 1 or 2 poorly defined glands on abaxial surface near base; *petals, stamens, styles,* and *stigmas* not seen; *ovary* fully inferior, ca. 2 mm long. *Fruit* oblate; nut 10–12 × 9–12 mm, on sides longitudinally 5-crested with crests ca. 2 mm high, formed from decurrent margins of accrescent sepals; persistent sepal limbs spreading, subcoriaceous, spathulate to oblanceolate, unequal, larger 3 sepals 35–45 × 11–16 mm, smaller 2 sepals 22–30 × 6–8 mm; pericarp drying brown, coriaceous; *seed* not seen.

Distribution, phenology, and habitat. Wet evergreen forest of Udzungwa Mountains, south-central Tanzania, at 1100–1310 m [900–1500 m, Cheek et al., 2000]; collected in flower bud in August, in fruit in February and December.

Provisional conservation status. With an EO of less than 5000 km² and occurring only in the Udzungwa Mountains National Park, Tanzania, outside of which its habitat is threatened (Critical Ecosystem Partnership Fund, 2003), and already listed as potentially threatened (Gereau & Luke, 2003): Endangered (B1ab); Cheek (2000: 875) proposed a status of Endangered (EN A1c).

Cheek et al. (2000) noted accurately that this species is poorly known. They reported its altitudinal distribution as 900–1500 m, but listed vouch-

er specimens only from 1100–1500 m, and the label data on the specimens examined indicated an altitudinal range of 1100–1310 m. In any case, as they also noted, the elevational range of *Ancistrocladus tanzaniensis* is unusually high among the African species of the genus.

Cheek et al. (2000: 208) described the fruits of this species as "falsely inferior," but their reason for this is not clear. This same description was given by Léonard (1984, 1986) for the fruits of *Ancistrocladus robertsoniorum* because the ovary of that species is only partially inferior in flower while the fruit appears to be fully inferior due to subsequent upward growth of its accrescent calyx tube. The situation may be similar in *A. tanzaniensis*, but Cheek et al. (2000) reported that they were not able to study flowers or buds. The ovary of *A. tanzaniensis* appears to be fully inferior in the flower buds studied.

Cheek et al. (2000: 210) separated *Ancistrocladus tanzaniensis* from the Kenyan species *A. robertsoniorum* by its leaf pits "so dense and conspicuously black in the Kenyan species (seen in every specimen at Kew) as to be visible with the naked eye whereas in the Tanzanian species only a few pits are present near the stem on the lower surface of the leaf (sometimes a few very thinly scattered over the leaf), and can only be detected with difficulty with a lens." They refer here to the small pits ("each containing a glandular hair"), which are densely distributed on the leaves of both species. With more specimens now available there appears to be more variation than they observed in the density and distribution of these small pits in *A. tanzaniensis*; in general these pits are more evident in younger leaves, and their degree of wax filling seems to be correlated with leaf age. The distribution and appearance of the large pits are also similar in the leaves of these two species.

Additional specimens examined. TANZANIA. **Iringa:** Iringa Rural Dist., Udzungwa For. Res. above Chita JKT [military camp], *F. Mbago 1803* (DSM, MO); steep slopes on W-facing escarpment, *C. Frimodt-Møller et al s.n. in TZ-560* (DSM).

16. Ancistrocladus tectorius (Lour.) Merr., Lingnan Sci. J. 6: 329. 1928 [1930]. *Bembix tectoria* Lour., Fl. Cochinch. 282. 1790. TYPE: Cochinchina [Vietnam]. Without locality, s.d., *J. de Loureiro s.n.* (holotype, BM!).

Ancistrocladus extensus Wall. ex Planch., Ann. Sci. Nat. Bot., sér. 3, 13: 318. 1849. TYPE: Burma [Myanmar]. [Probably Mon State:] Amherst, prov. Martaban, s.d., *N. Wallich Numer. List 1052.1* (holotype, K not seen, photo MO!; isotypes, BM [2]!, E!, K not seen, photo MO!, K-WALL!, photo MO!).

Ancistrocladus pinangianus Wall. ex Planch., Ann. Sci. Nat. Bot., sér. 3, 13: 318. 1849. *Ancistrocladus extensus* Wall. ex Planch. var. *pinangianus* (Wall. ex Planch.) King, J. Asiat. Soc. Bengal 42: 137. 1893. TYPE: Malaysia. Pilau Pinang: Penang [Pinang], s.d., *G. Porter s.n. in Wallich Numer. List. 1054* (holotype, K!; isotypes, BM!, BR!, C!, E!, K!, K-WALL!, P!).

Ancistrocladus cochinchinensis Gagnep., Notul. Syst. (Paris) 1: 115. 1909. Syn. nov. TYPE: Vietnam. Bin Dinh, in montibus, 300 m, Mar. 1867, *L. Pierre 16* (lectotype, designated by Gereau (1997: 243), P!; syntypes, A!, C [2]!, K not seen, L!, P!, US!).

Ancistrocladus harmandii Gagnep., Notul. Syst. (Paris) 1: 114. 1909. Syn. nov. TYPE: Laos. Koukou: bassin du Sé-moun [Mun River], Jan. 1877, *Bro. F. J. Harmand 989* (holotype, P!; isotype, K not seen).

Ancistrocladus hainanensis Hayata, Icon. Pl. Formosan. 3: 46. 1913. TYPE: China. South Central: Hainan Island, Ngai District, Fung Leng, 29 Aug. 1932, *S. K. Lau 455* (neotype, designated here, KYO!).

Ancistrocladus carallioides Craib, Bull. Misc. Inform. 1925: 19. 1925. Syn. nov. TYPE: Thailand. Northern Region: Nan, Doi Tiu, 9 Mar. 1921, *A. F. G. Kerr 5053* (holotype, K not seen; isotype, BM!).

Juvenile plants unknown. *Juvenile leaves* unknown. *Adult stems* climbing to 20 m high, to 1 cm diam. [probably becoming larger but no data], with bark purplish brown, smooth to roughened, bearing some scattered leaves and lateral branchlets to 23 cm long, these each bearing 1 to several hooks and sometimes a terminal cluster of leaves; *hooks* recurved to spiraling, 6–20 mm diam. *Adult leaves* drying papyraceous to chartaceous, rather shiny on both surfaces, in life not seen, drying discolorous, brown to dark brown above, paler brown to yellow-brown below; pits dimorphic, small pits frequent on both surfaces, large pits 0.2–0.5 mm diam., circular, occasional on adaxial surfaces; midrib adaxially shallowly sulcate, abaxially prominent, terminating in a tiny gland; secondary veins prominulous on both surfaces; tertiary veins reticulated and prominulous on both surfaces; margins plane to thinly revolute; *stem leaves* with persistence unknown, elliptic to oblong or oblanceolate, sometimes falcate, 5–34 × 1.1–8.3 cm, L/W 2.2–6.8, at apex acute to rounded, at base cuneate to acute; secondary veins (6 to)13 to 16 pairs, with intramarginal vein not evident; *leaves at branchlet apices* with persistence unknown, elliptic to obovate, 7.0–38.0(–50.2) × 2.1–9.3(–11.7) cm, L/W (1.7–)2.0–5.6(–6.1), at apex acute to rounded and sometimes abruptly shortly acuminate, at base sometimes long-attenuate; secondary veins 6 to 14(to 22) pairs, with intramarginal vein situated 0–2 mm from margin. *Inflorescence* lax to congested, paniculate, lateral among leaves at apices of branchlets, occasionally bearing hooks, without bracteal leaves; peduncle 0.5–2.3 cm long, often flexuous; branched portion

corymbiform, 5.5–12.0 × 6–16 cm, dichotomously branched; bracts triangular to ovate, 0.2–2.4 × 0.2–1.5 mm, at apex acute and erose, at base obtuse, abaxially eglandular or with 1 or 2 circular glands occupying ½–¾ of surface; pedicels 0.3–3.0 mm long. *Flowers* all pedicellate; *sepals* 5, suborbicular to elliptic-oblong, rounded at apex, at base rounded to truncate and shortly decurrent on ovary, brownish purple, abaxially eglandular or with 1 to 4 raised glands ca. 0.2 mm diam., unequal, larger 3 sepals 4.2–5.5 × 1.8 mm, smaller 2 sepals 3.2–4.5 × 2.2 mm; *petals* 5, convolute, suborbicular, cream, pink, green, or white-yellow to dark red, 5.0–6.0 × 2.0–3.0 mm; *stamens* 10 in 1 whorl, purple; filaments thickened at base, dimorphic, the shorter 0.3–1.2 mm long, the longer 1.1–2.0 mm long; anthers 0.4–0.8 mm long; *ovary* fully inferior, 1–3 mm long; styles 3, ca. 1 mm long, stigmas ca. 0.2 mm long. *Fruit* turbinate; nut 5–9 × 5–10 mm, on sides 5-ridged by decurrent margins of accrescent sepals; persistent sepals spreading, chartaceous to papyraceous, unequal, larger 3 sepals spathulate, 30–56 × 10–17(–25) mm long, smaller 2 sepals narrowly oblong to spathulate, 20–30(–40) × 5–12(–19) mm; pericarp drying golden rust-brown, coriaceous; *seed* pale yellow, not seen.

Habitat, phenology, and distribution. Lowland to premontane evergreen but rather dry forests at 0–1524 m, on red basaltic, granitic, or sandy to clay soils, Myanmar, Thailand, and Cambodia through Laos to China (Hainan Island) and Vietnam, and south through Malaysia to Singapore, the Andaman and Nicobar Islands of India, and Sumatra and Borneo of Indonesia; collected in flower and fruit throughout the year, apparently sometimes concurrently.

This species circumscription here concords with that of Steenis (1948). Steenis (1948) reported this species additionally from Borneo; we have seen no specimens from there but have no reason to doubt this report. Loureiro's specific epithet apparently refers to the local use of *Ancistocladus tectorius* in the construction of the roofs of houses. Keng (1967) studied the vegetative and reproductive morphology and anatomy of this species in detail.

There is notable variation in *Ancistrocladus tectorius* in several morphological features, in particular the degree of development of the bracts and the presence and number of abaxial sepal glands. Most plants can readily be assigned to one of two forms, but these two forms are linked by a number of intermediate specimens and thus are not recognized taxonomically here. A number of plants, including nearly all of those from China through Vietnam and many from Malaysia, Singapore, and Sumatra, resemble *A. heyneanus* in having one to three well-developed, marginate glands on the outer three sepals, the flowers subsessile or shortly pedicellate (i.e., pedicels up to 1.5 mm long), and the inflorescence bracts numerous, well developed (0.5–2.4 mm long), abaxially bearing one to three marginate glands, and usually persisting while the fruits mature. These plants resemble the type specimens of *A. tectorius*, *A. cochinchinensis*, and *A. harmandii*. Another group of plants found in Malaysia, Sumatra, Singapore, and the Andaman Islands differs in having sepals without abaxial glands, pedicels 1.5–3.0 mm long, and the bracts few, small (0.2–1.0 mm long), usually eglandular, and often caducous at or shortly after anthesis. These plants resemble the type of *A. pinangianus*.

Wallich's specimens included *Ancistrocladus* material that he treated as his *Wallich Numer. List 1052* and called "Ancistrocladus extensus Wallich" though without publishing a validating description or diagnosis for this name. This catalogued species included material from two different collections, *Wallich Numer. List 1052.1* from Amherst, a British station in Burma (today Myanmar) that was presumably collected by Wallich himself, and *Wallich Numer. List 1052.2* from Pundua, a British Station in notheastern India, collected by Wallich's collaborator there, Francis da Sylva. These collections are notably different in appearance, but the specimens of *Wallich Numer. List 1052.1* comprise hook-bearing branchlets with young to fully mature fruits and several robust vegetative apices while the specimens of *Wallich Numer. List 1052.2* comprise hook-bearing branchlets with flowers and a few immature fruits. Thus these collections lack comparable reproductive structures and consequently are difficult to compare. Planchon (1849) concluded that these gatherings did represent two different species, and described *Wallich Numer. List 1052.1* as *A. extensus* Wall. ex Planch. and *F. da Sylva in Wallich Numer. List 1052.2* as *A. wallichii* Planch. Planchon's publication of *A. wallichii* was apparently not widely noted, however, and specimens of *Wallich Numer. List 1052.2* as well as later, sometimes similar collections continued to be identified as "A. extensus Wallich." We here concur with Steenis (1948) and consider *A. extensus* a taxonomic synonym of *A. tectorius*. However, we are unable to conclusively determine the identity of *A. wallichii*, and thus here consider it a name of dubious identity as discussed further below, in that section.

Gereau (1997) noted that *Z. Katsumada s.n.*, the type designated in the protologue of *Ancistrocladus hainanensis*, has not been located at KYO, SING,

or TI. No illustration was published with the name, and no other original material has been found. *S. K. Lau 455* is a widely distributed flowering collection (duplicates seen at A, BM, E, KYO, MO, P, TI, US) that agrees in all respects with the protologue of *A. hainanensis*, and the duplicate of this collection at KYO is here selected as the neotype.

Selected specimens examined. CAMBODIA. **Phnom Penh:** forêts de Phnom Penh, *Béjaud 254* (P). **Siem Reab:** Savay Leu District, ca. 70 km NE Siem Reap [sic] proper, 14°00′N, 104°30′E, *A M. Huq et al. 10836* (F, MO). CHINA. **Hainan:** Ngai District, Yeung Ling Shan, *S. K. Lau 19* (A, BM, E, MO, P, TI, US). INDIA. **Andaman & Nicobar Islands:** Anikehet, Cadell Gunj, South Andamen, *Dr. King's collector s.n.* 7–3–1891 (SING), 20–2–1892 (P), 22–4–1893 (P, US), 4–8–1894 (P). INDONESIA. **Barat:** Karimata Archipelago, Poulan Karamata, *Mondi 158* (SING). **Sumatera Selantan:** Bangka, Lobokbesar, *A. J. Kostermans & Anta 867* (A, P, PNH, SING). **Sumatera Utara:** Laboehan Batoe, Kota Pinan Dist., Sboengan (on the Soengai Kanan), *R. S. Toroes 3730* (A, US). LAOS. Province unknown: vers Ban Bo Ken et Ban [Xa] Phang Meuk, *P. Tixier 26-1-56-03* (P). **Savannakhét:** Km 20 de la route No. 10 près Savannakhét, *M. Poilane 11679* (P), *11954* (P). MALAYSIA. **Johore:** G. Ledang, Mt. Ophir, *B. C. Stone 10721* (ANSP, MO). **Kedah:** Compt 11, Gunong Raya F.R., Pulau Langkawi, *S. Chelliah FRI-6912* (SING). **Kelantan:** Ulu Sungei Lobir near Kuala Sepia, *B. C. Stone 7351* (ANSP). **Negeri Sembilan:** Kg. Sungai Layang, Rembau, *S. C. Chin & Mustafa 3253* (A, ANSP, MO). **Pahang:** Deserah, Kunatan, *M. R. Hendersen 22743* (SING). **Perak:** Sg. Plus, Chior F.R., Sg. Siput, *F. S. P. Ng FRI-51* (A). **Pulau Pinang:** Penang [Pinang], Pulau Boetong, *C. Curtis s.n.* (SING). **Selangor:** Kipong Plantation, *A. Hamid 33859* (SING). **Trengganu:** Jambu Bongkok seashore, *J. Carrick 779* (ANSP). MYANMAR [BURMA]. Probably **Mon:** Amherst, prov. Martaban, *Wallich Numer. List 1052.1* (BM, E, K photos MO, K-WALL photo MO). SINGAPORE. Changi, *H. N. Ridley 1901* (BM), *3810* (BM), *5918* (BM). THAILAND. **Central Region:** Prachuap Kiri Khan Prov., Huai Yang waterfall S of Prachuap, 11°40′N, 99°50′E, *C. F. van Beusekom & T. Santisuk 2758* (C, E, KYO, P). **Northeastern Region:** Nakhon Ratchasima Prov., PakThong Chai, Khao Pha Yom, *S. Phengnaren 489* (E, P). **Northern Region:** Nan Prov., Doi Tui, *A. F. G. Kerr 5053* (BM, K). **Southeastern Region:** Trat Prov., Khao Chawng, Khlawng, *B. Sawngkachun 404* (A). **Southern Region:** Songkla Prov., Satingpra District, Ko Kobe (Kobe Island), Lake Songkla, *P. Sirirugsa 754* (ANSP). VIETNAM. **Bac Giang:** Tonkin [Bac Phan], environs Su Pho Vi, *M. Pételot 4813* (P, US). **Binh Dinh:** Binh Dinh [An Nhon], *Pierre 1734* (A, P). **Da Nang:** Tourane [Da Nang], *J. Clemens & M. S. Clemens 3350* (A, BM, MO, P, US). **Kom Tum:** Dak Gley District, 10–12 km SE of Dak Gley town, *L. Averyanov et al. VH2245* (MO).

Names of Dubious Identity

Ancistrocladus stelligerus Wall. ex DC., Prodr. 16(2): 603. 1868. TYPE: Myanmar [Burma]. Prov. Martaban, s.d., *Wallich Numer. List. 1053* (lectotype, designated here, G-DC not seen, microfiche MO!).

In the microfiche of the G-DC herbarium (Conservatoire et Jardin botaniques de la Ville de Genève, 1962), there are three specimens labeled "Ancistrocladus stelligerus Wall., De Cand. prodr. 16.2. 603 no. 6" but none of these is visibly marked "Wallich 1053." One specimen has relatively broad branchlet leaves and an additional label with the words "A. stelligerus (Fructus unicus)," but no fruit is visible in the photograph. A second specimen has relatively narrow branchlet leaves and an additional label with the words: "Ancistrocladus stelligerus Wall., Comp. angl. des Indes orient. 1830." A third specimen has relatively narrow stem leaves and hooked branchlets bearing immature, narrow leaves, with no additional label. Only the first of these three specimens agrees in leaf shape and dimensions with the protologue of *Ancistrocladus stelligerus*, and the notation "Fructus unicus" on the specimen corresponds to the protologue: "Fructus in specimine unicus." We therefore select this broader-leaved specimen at G-DC as the lectotype of *A. stelligerus*. The other two specimens are similar to *A. attenuatus* or *A. griffithii* in leaf characters and are excluded from this typification. In addition, two specimens at BM labeled "Wall. cat. 1053" (BM 012422) and "1053 Wallich" (BM 012423) are excluded from the typification of *Ancistrocladus stelligerus*, as is the single specimen at E labeled "1053 Ancistrocladus stelligerus Wall [three illegible initials]" and (on a separate label) "Herb. Walker Arnott." There is no evidence that Candolle examined any of the excluded specimens of *Wallich Numer. List 1053* at BM and E, all conflict with the protologue of *A. stelligerus* in leaf shape and dimensions, and none can be positively identified to species. We have not had the opportunity to examine the duplicate of *Wallich Numer. List 1053* at K-WALL, which should be considered an isolectotype only if it resembles the lectotype in leaf characters, but otherwise should also be excluded from this typification.

The foliage of the lectotype of *Ancistrocladus stelligerus* appears to fit well within our circumscription of the widespread species *A. tectorius*. However, the description of the fruit in the protologue of *A. stelligerus* is consistent instead with our circumscription of *A. griffithii*. Because this combination of leaf and fruit characters is not present in any known species of *Ancistrocladus*, it is highly probable that the description of *A. stelligerus* was based on a mixed collection, and we here treat *Ancistrocladus stelligerus* as a name of doubtful application. This name was inadvertently omitted by Gereau (1997).

Ancistrocladus wallichii Planch., Ann. Sci. Nat. Bot., sér. 3, 13: 319. 1849. TYPE: India/Bangladesh Border. Pundua, s.d., *F. da Sylva s.n. in Wallich, Numer. List. 1052.2* (holotype, K not seen, photo MO!; isotypes, C!, GH!, K-WALL!, photo MO!).

The name *Ancistrocladus wallichii* has long been applied to Asian plants with notably long narrow leaves, in particular those treated here in *A. attenuatus* and *A. griffithii*. However, the type specimens of *A. wallichii* have leaves 5.5–35.0 cm long, none of them particularly narrow, lack flowers and fruits, and cannot be positively identified as any of the species recognized in this present treatment. Consequently the identity of *A. wallichii* is not clear at all.

However, there have been varied applications of the name *Ancistrocladus wallichii*. This name has at times been equated with *A. extensus*, a synonym of *A. tectorius*; this particular confusion apparently stems from the numbering of the type specimens of *A. wallichii* and *A. extensus* as *Wallich Numer. List 1052.1* and *Wallich Numer. List 1052.2*, respectively, which implied that they represent the same species; this situation is outlined in more detail in the discussion under *A. tectorius*, above. The name *A. wallichii* has also been equated with *A. griffithii*, apparently due largely to the mistaken labeling of the specimens numbered *Wallich Numer. List 1053* with this second name; but as outlined in the discussion under *A. stelligerus* above, these particular specimens are here excluded from the type collection of *A. stelligerus*. These various incorrect applications of this name have generated confusion in its application; for example, in Das (1993) the actual type specimens of *A. wallichii* would key out separately from the plants treated under this name.

The type locality of *Ancistrocladus wallichii* is Pundua, India. This locality does not appear on modern maps, but was a town located in the Ganges River valley near the border of what was then Bengal and Assam, and is now Bangladesh and Assam State, India (Rees, 1819, as "Pundna"; Candolle & Radcliffe-Smith, 1981). There Francis da Sylva (or Silva, Silhet, or Sylhet) collected for Wallich (Candolle & Radcliffe-Smith, 1981). We have seen no other *Ancistrocladus* species from that region; the closest documented species to this region are *A. attenuatus*, known from Calcutta in the lower Ganges basin, and *A. griffithii* and *A. tectorius*, known from Myanmar. If the name *A. wallichii* were synonymous with *A. attenuatus*, it would be the older name for that species and thus would have priority.

Excluded Species

Ancistrocladus pentagynus Warb., Bot. Jahrb. Syst. 13: 383. 1891. TYPE: not designated.

As noted by Gereau (1997), Steenis (1948) cited Hallier (1923: 77) in considering this a species of *Durandea* Planch. (Linaceae).

Ancistrocladus sagittatus Wall. ex Planch., Ann. Sci. Nat. Bot., sér. 3, 13: 319. 1849. TYPE: Singapore. Without locality, s.d., *Wallich Numer. List 1055* (not seen).

As noted by Gereau (1997), Steenis (1948) placed this name in synonymy with *Tetramerista glabra* Miq. (Tetrameristaceae).

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Appendix I. Keys to *Ancistrocladus* Species by Continent

1. key to species of *Ancistrocladus* in Asia

1a. Stamens 5; fruit with nut body ca. 20 × 15–19 mm; plants of Sri Lanka . . . . . 9. *A. hamatus* (Vahl) Gilg
1b. Stamens 10 to 15 (number unknown in *A. griffithii*); fruit with nut body 5–10 × 5–14 mm; plants of continental Asia and islands east of Sri Lanka.
2a. Fruit with accrescent sepals subequal, 5–15 × 4–8 mm; branchlet leaves 10.0–45.0 × 1.5–5.4 cm, with L/W 4.3–11.5.
3a. Branchlet leaves with secondary veins plane on adaxial surface, very slightly prominulous on abaxial surface; sepals in flower 4–9 mm long; petals 5–9 mm long; filaments 4–6 mm long; fruit with nut body ca. 10 × 14 mm, accrescent sepals spathulate . . . . . 2. *A. attenuatus* Dyer
3b. Branchlet leaves with secondary veins prominulous on both surfaces; sepals in flower 1.9–2.2 mm long; petals ca. 1.7 mm long; filaments 0.2–0.5 mm long; fruit with nut body 5–6 × 8–10 mm, accrescent sepals oblanceolate . . . . . 7. *A. griffithii* Planch.
2b. Fruit with accrescent sepals markedly unequal in size (e.g., Fig. 1F, G), the larger ones 25–56 × 10–25 mm; branchlet leaves 7.0–50.2 × 2.1–11.7 cm, with L/W 1.7–6.3.
4a. Branchlet leaves with midrib adaxially plane to a little prominulous, intramarginal vein situated 2–4 mm from margin; sepals in flower 6.0–6.5 mm long; petals 6–7 mm long; fruit with larger accrescent sepals 25–40 × 12–17 mm, the smaller accrescent sepals 19–26 × 5–7 mm; plants of the Indian subcontinent . . . . . 10. *A. heyneanus* Wall. ex J. Graham
4b. Branchlet leaves with midrib adaxially shallowly sulcate, intramarginal vein situated 0–2 mm from margin; sepals in flower 3.2–5.5 mm long; petals 5–6 mm long; fruit with larger accrescent sepals 30–56 × 10–25 mm, smaller accrescent sepals 20–40 × 5–19 mm; plants of Asia east of the Indian subcontinent . . . . . 16. *A. tectorius* (Lour.) Merr.

2. key to species of *Ancistrocladus* in Africa

1a. Adult leaves with large pits usually oblong, (0.5–)2.0–4.0 × 0.5–1.0 mm; branchlet leaves narrowly oblanceolate to elliptic-oblanceolate, with L/W 3.5–15.5; inflorescence bracts spathulate, elongated at base, by late anthesis becoming cochleate to clavate; stems smooth or with small epidermal protuberances . . . . . 12. *A. letestui* Pellegr.
1b. Adult leaves with large pits circular to elliptic or oval, 0.1–1.0 mm diam.; branchlet leaves oblanceolate to elliptic or obovate, with L/W 1.3–5.8; inflorescence bracts triangular to ovate, not elongated at base; stems smooth.
2a. External sepals without abaxial glands (visible in flower and young fruit).
3a. Fruit with nut body 5–8 × 3–6 mm, with smaller accrescent sepals 5–20 mm long.
4a. Adult leaves drying usually somewhat discolorous, dark brown above, lighter brown beneath, or sometimes concolorous and gray-tan on both sides; branchlet leaves with secondary veins 7 to 16 pairs, with intramarginal vein situated 2–4 mm from margin; inflorescence bracts abaxially with a gland covering ca. ½ the surface; pedicels 2–5 mm long; petals imbricate, ca. 8.1 mm long; filaments 4.5–5.0 mm long; styles ca. 5 mm long; plants of Nigeria, Cameroon, and Gabon . . . . . 8. *A. guineensis* Oliv.
4b. Adult leaves drying discolorous, dark brown above, yellow-green beneath; branchlet leaves with secondary veins 10 to 25 pairs, with intramarginal vein situated 0–1 mm from margin; inflores-

cence bracts eglandular; pedicels 5–12 mm long; petals convolute, 5–7 mm long; filaments 1.0–2.0 mm long; styles ca. 3 mm long; plants of coastal Kenya . . . . 14. *A. robertsoniorum* J. Léonard

3b. Fruit with nut body 10–12 × 9–12 mm, with smaller accrescent sepals 11–30 mm long.

5a. Branchlet leaves oblanceolate, with L/W 2.9–4.2; inflorescence with peduncle 4.0–13.0 cm long, branched portion 7–16 × 12–20 cm, bracts 0.5–1.0 mm long, abaxially eglandular; plants of Nigeria and Cameroon . . . . . 11. *A. korupensis* D. W. Thomas & Gereau

5b. Branchlet leaves oblanceolate to narrowly so, with L/W 4.0–5.8; inflorescence with peduncle 1.1–3.5 cm long, branched portion 3.5–8.0 × 6–11 cm, bracts 1.1–1.8 mm long, abaxially with a gland occupying ⅓–⅔ of surface; plants of Tanzania . . . . . 15. *A. tanzaniensis* Cheek & Frim.

2b. External sepals with 1 to 6 abaxial glands (visible in flower and young fruit).

6a. Inflorescence subcapitate to congested-cymose, solitary, apparently terminal, subsessile or with peduncle to 0.5 cm long . . . . . 1a. *A. abbreviatus* Airy Shaw subsp. *abbreviatus*

6b. Inflorescence paniculate to corymbiform with ultimate axes sometimes racemiform, solitary to several, lateral, subterminal or apparently terminal, with peduncle 1–13 cm long.

7a. Sepals distinctly unequal in size in flower and fruit, with three larger and two smaller.

8a. Sepals 4 or 5, in flower [6.5–9.0]9.5–14.2 mm long; petals 4 or 5, in flower [9.0–]9.5–12.0 mm long . . . . . 6. *A. grandiflorus* Cheek

8b. Sepals 5, in flower 2.5–6.0 mm long; petals 5, in flower 2–10 mm long.

9a. Adult leaves drying usually somewhat discolorous, dark brown above, lighter brown beneath, or sometimes concolorous and gray-tan on both sides; pedicels 2–5 mm long; fruit with nut body 5–8 × 3–6 mm . . . . . 8. *A. guineensis* Oliv.

9b. Adult leaves drying discolorous, dark green above, yellow-green beneath; pedicels 3–9 mm long; fruit with nut body 10–12 × 9–12 mm.

10a. Branchlet leaves oblanceolate, with L/W 2.9–4.2; inflorescence with peduncle 4.0–13.0 cm long, branched portion 7–16 × 12–20 cm, bracts 0.5–1.0 mm long, abaxially eglandular; fruiting sepals chartaceous to papyraceous; plants of Nigeria and Cameroon . . . . . 11. *A. korupensis* D. W. Thomas & Gereau

10b. Branchlet leaves oblanceolate to narrowly so, with L/W 4.0–5.8; inflorescence with peduncle 1.1–3.5 cm long, branched portion 3.5–8.0 × 6–11 cm, bracts 1.1–1.8 mm long, abaxially with a gland occupying ⅓–⅔ of surface; fruiting sepals subcoriaceous; plants of Tanzania . . . . . 15. *A. tanzaniensis* Cheek & Frim.

7b. Sepals equal to subequal and continuously grading in size in flower and fruit.

11a. Peduncle 1.0–2.1 cm long.

12a. Branchlet leaves very shortly and obtusely acuminate to rounded at apex; petals 6–10 mm long; styles 3; fruit with nut body 8–15 × 10–15 mm; plants of Nigeria . . . . . 1b. *A. abbreviatus* Airy Shaw subsp. *lateralis* Gereau

12b. Branchlet leaves usually acute to long-acuminate at apex; petals 2–3 mm long; style 1; fruit with nut body 4–5 × 7–8 mm; plants of Central Africa . . . . . 5. *A. ealaensis* J. Léonard

11b. Peduncle 2.2–11.0 cm long.

13a. Petals 5–11 mm long; fruit unknown; plants of West Africa . . 3. *A. barteri* Scott-Elliot

13b. Petals 2–4 mm long; fruit with accrescent sepals 5–13 mm long; plants of Central Africa.

14a. Styles 3; filaments apparently equal, ca. 1.5 mm long . . . . . 4. *A. congolensis* J. Léonard

14b. Style 1; filaments dimorphic, 0.4–1.2 mm long.

15a. Branchlet leaves narrowly elliptic to elliptic-oblong or oblanceolate, with L/W 2.5–4.5, at apex usually acute to long-acuminate, with intramarginal vein situated 3–7 mm from margin; inflorescence with branched portion 3–6 cm long, bracts without pits; sepals 2.5–5.0 × 2.0–3.0 mm; petals 2–3 × 2–3 mm; filaments weakly dimorphic, the shorter 0.5–0.7 mm long, the longer 0.8–1.0 mm long; anthers ca. 0.5 mm long; style 1.0–1.5 mm long; fruit with nut body 4–5 × 7–8 mm, with slender low ridges and the sides otherwise flat or gently concave . . . . . 5. *A. ealaensis* J. Léonard

15b. Branchlet leaves obovate, with L/W 2.1–3.5, at apex obtuse to rounded and sometimes abruptly shortly acuminate, with intramarginal vein situated 1–3 mm from margin; inflorescence with branched portion 6–24 cm long, bracts with 1 or usually 2 pits on each side; sepals 5.0–9.0 × 3.0–6.0 mm; petals 3–4 × 3–4 mm; filaments strongly dimorphic, the shorter ca. 0.4 mm long, the longer ca. 1.2 mm long; anthers ca. 1.0 mm long; style 2.0–3.0 mm long; fruit with nut body 10–18 × 12–18 mm, with markedly thickened ridges enclosing deeply sculpted sides . . . . . 13. *A. likoko* J. Léonard

Appendix II. Numbered Collections of *Ancistrocladus* Studied.

List of species

Species are numbered alphabetically as in the text. The name in bold is newly published in this article.

1. *Ancistrocladus abbreviatus* Airy Shaw
   1a. subsp. *abbreviatus*
   1b. subsp. *lateralis* Gereau
2. *A. attenuatus* Dyer
3. *A. barteri* Scott-Elliot
4. *A. congolensis* J. Léonard
5. *A. ealaensis* J. Léonard
6. *A. grandiflorus* Cheek
7. *A. griffithii* Planch.
8. *A. guineensis* Oliv.
9. *A. hamatus* (Vahl) Gilg
10. *A. heyneanus* Wall. ex J. Graham
11. *A. korupensis* D. W. Thomas & Gereau
12. *A. letestui* Pellegr.
13. *A. likoko* J. Léonard
14. *A. robertsoniorum* J. Léonard
15. *A. tanzaniensis* Cheek & Frim.
16. *A. tectorius* (Lour.) Merr.

Asterisks indicate type specimens. Numbers in parentheses indicate identifications, following the species list above.

Abbiw, D. K. 135 (3); Adam, J.-G. 5238 (3), 23228 (3), 24219 (3), 24790 (3), 28632 (3), 26864 (3); Aké Assi, L. 17146 (3), 17768 (3); Akpaaba, G. K. 219 (1a); Annandale, N. s.n. 24 Jan. 1916 (16); Anonymous 340 (16); Averyanov, L. et al. VH 2245 (16), VH 4300 (16).

Balansa, B. 3837 (16), 3838 (16); Baldwin, J. T., Jr. 5839* (3), 10603 (1a), 10756 (3), 10984 (3), 11016 (3), 14068 (3); Barter, C. 1699* (1b); Batton Pool, A. H. s.n. 10–17 Feb. 1940 (16); Beddome, R. H. 467 (10), 446 (10); Berhaut, R. P. 7105 (3), 7406 (3), 7407 (3), 7112 (3); Bernardi, L. 16073 (9); Bos, J. J. 2614 (3); Breteler, F. J. 5719 (8); Breteler, F. J. & J. J. F. E. de Wilde 623 (4); Breteler, F. J. & C. Jongkind 10137 (4); Breteler, F. J. et al. 1186 (12); Bünnemayer, H. 5971 (16).

Carrick, J. 779 (16), 2470 (16); Chelliah, S. FRI-6912 (16); Chen, N. 44617 (16); Chen, S. 11516 (16); Chen, Z. 30039 (16); Chevalier, A. 12097 (1a), 28142 (5), 28208 (5), 31864 (7), 37039 (16), 38617 (16), 40725 (16); Chillou, J. 984 (1a); Chinm S. C. & Mustafa 3253 (16); Chun, N. K. & C. L. Tao 44617 (16); Clemens, J. & M. S. Clemens 3550 (16); Collins, Mrs. D. J. 369 (16), 859 (16), 951 (16), 1134 (16); Congdon, G. 947 (16), 1080 (16); Contest-Latour, E. 311bis (16); Coray, L. 1862 (16); Coûteaux, G. 41 (5); Cramer, L. H. 4179 (9); Curtis, C. 774 (16), 2936 (16).

Daramola, B. O. 449 (8); Deighton, F. C. 2589* (1a); Deng, L. 3138 (16); de Wilde, J. J. F. E. 801 (3), 3314 (1a); Didichren, S. 3419 (16); Drummond, R. B. & J. H. Hemsley 3936 (14).

East Hainan Team 94 (16); Ejiofor, M. C. FHI-32015 (8); Emwiogbon, J. A. 344* (1b); Enti, A. A. FE-1317 (3), FE-1906 (1a); Evrard, C. 1463 (5), 1765 (5), 2097 (13), 2218 (13), 2931 (5), 3720 (4), 3866 (5), 4552 (5), 4843 (5), 5950 (5).

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Hall, H. & D. Abbiw GC-44711 (3); Hall, H. & L. Aké Assi GC-45772 (3); Hall, H. & A. A. Enti GC-39985 (1a); Hallé, N. 1609 (5), 1680 (5), 2648 (12), 3955 (12); Hallé, N. & A. Le Thomas 287 (4), 477 (8); Hallé, N. & J.-F. Villiers 4382 (8), 4695 (12), 5391 (5); Hamid, A. 33859 (16); Hamill, I. 13137 (16); Haniff, M. 3846 (16), 15512 (16); Hansen, B. & T. Smitinand 11813 (16), 11835 (7); Harley, W. J. 1397 (1a); Harmand, Bro. F. J. 178 (16), 989* (16), 1181 (16); Harris, D. J. & J. M. Fay 291 (5), 1424 (5), 643 (5); Helfer, J. W. 724* (2), 720 (7), 723 (7); Henderson, M. R. 22743 (16); Herb. Hongkong 2121A (16); Holmberg, P. J. 771 (16); Hou, K. = F. C. How; How, F. C. 70418 (16), 70604 (16), 71616 (16); Huang, Z. 33144 (16).

Ibenegbu, D. A. FHI-26206 (1b).

Jaeger, P. 7441 (3); Jans, E. s.n. 23–5–48 (13), 879 (5); Jones, A. P. D. 2715 or FHI-621 (1b), 2807 or FHI-5898 (1b); Jones, A. P. D. & C. F. Onochie FHI-16641 (8), FHI-16757 (8), FHI-17026 (8).

Kadim [bin Tassim] & Noor KN-552 (16); Keay, R. W. J. FHI-28061 (8); Keith, Dr. A. 148 (16); Kerr, A. F. G. s.n. 10 Apr. 1920 (16), s.n. 5 Apr. 1923 (16), 37 (16), 595 (16), 1370 (16), 5053* (16), 7006 (7), 7943 (7), 13972 (16), 14829 (16), 16557 (16), 18030 (16), 20727 (16), 21332 (16), 21661 (2); King, Dr. [Sir George]'s Collector 5533 (16); Ko, S. P. 52272 (16); Kochummen, K. M. FRI-29404 (16); Kostermans, A. J. 24676 (9); Kostermans, A. J. & Anta 867 (16); Koyama, H. et al. 33051 (16), 33056 (16).

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Rischer, H., G. Heubl, H. Meimberg, M. Dreyer, H. A. Hadi & G. Bringmann. 2005. *Ancistrocladus benomensis* (Ancistrocladaceae): a new species from Peninsular Malaysia. Blumea 50: 357–365.

PHYLOGENY, MORPHOLOGICAL EVOLUTION, AND SPECIATION OF ENDEMIC BRASSICACEAE GENERA IN THE CAPE FLORA OF SOUTHERN AFRICA[1]

Klaus Mummenhoff,[2]
Ihsan A. Al-Shehbaz,[3]
Freek T. Bakker,[4]
H. Peter Linder,[5]
and Andreas Mühlhausen[6]

Abstract

Heliophila (ca. 73 spp.), the ditypic *Cycloptychis* and *Thlaspeocarpa*, and the monotypic *Schlechteria*, *Silicularia*, *Brachycarpaea*, and *Chamira* are endemic to the Cape region of South Africa, where they are the dominant genera of Brassicaceae. They may be regarded as the most diversified Brassicaceae lineage in every aspect of habit, leaf, flower, and fruit morphology. The characters used in the separation of these genera and their species, especially fruit type (silique vs. silicle), dehiscence (dehiscent vs. indehiscent), compression (latiseptate vs. angustiseptate), and cotyledonary type (spirolobal, diplecolobal, twice conduplicate), have been used extensively in the delimitation of tribes. The relationship and taxonomic limits among these genera are unclear and controversial.

The present ITS study demonstrates the monophyly of tribe Heliophileae, with *Chamira* as sister clade. The other five smaller genera above are nested within two of the three main lineages of *Heliophila*, to which they should be reduced to synonymy. The current study reveals parallel evolution of fruit characters often used heavily in the traditional classification schemes of the family. However, the arrangement of species into three main clades largely corresponds with the distribution of morphological characters (e.g., habit, leaf shape, seed structure, inflorescence type, and presence/absence of basal appendages on the pedicels, petals, and staminal filaments) not adequately accounted for in previous studies. Estimation of divergence times of the main lineages of *Heliophila* is in agreement with recent estimations in other plant groups, all of which date the diversification against a background of aridification in the Pliocene and Pleistocene. Species of one main clade are perennial, microphyllous shrubs/subshrubs typically restricted to poor sandstone soils in the southwestern and western parts of the Cape Floristic Region of South Africa. Species of the other two clades are predominantly annuals that grow in more arid regions of Namibia and Namaqualand, as well as in the above sandstone areas of the Cape Region. The adaptive significance of various floral structures is discussed in terms of their possible role in the rapid diversification within *Heliophila*.

Key words: *Brachycarpaea*, Cape flora, Cape Floristic Region, *Chamira*, *Cycloptychis*, *Heliophila*, Heliophileae, ITS, phylogeny, radiation, *Schlechteria*, *Silicularia*, speciation, *Thlaspeocarpa*, *trn*L-F.

Seven genera of Brassicaceae, *Heliophila* (73 spp.), *Cycloptychis* (2 spp.), *Schlechteria* (1 sp.), *Silicularia* (1 sp.), *Thlaspeocarpa* (2 spp.), *Brachycarpaea* (1 sp.), and *Chamira* (1 sp.), are endemic to southern Africa (for author names of these genera and their species, see Table 1 and Appendix 1). Most species occur in the winter-rainfall area of the western Cape Floristic Region (CFR), where they represent the dominant Brassicaceae. Although several classification systems (Table 1) have been proposed (e.g., Hayek, 1911; Schulz, 1936; Janchen, 1942), the relationships among these genera remain unresolved. In a recent re-evaluation of the group, Appel and Al-Shehbaz (1997) placed the first six genera in the tribe Heliophileae and retained *Chamira* in the monotypic Chamireae. They

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[2] Department of Botany, Faculty of Biology/Chemistry, University of Osnabrück, Barbarastrasse 11, 49069 Osnabrück, Germany. Mummenhoff@Biologie.Uni-Osnabrueck.De.

[3] Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri, U.S.A. 63166-0299. ihsan.al-shehbaz@mobot.org.

[4] National Herbarium Nederland, Wageningen branch & Biosystematics Group, Wageningen University, Generaal Foulkesweg 37, 6703 BL Wageningen, The Netherlands. freek.bakker@wur.nl.

[5] Institute of Systematic Botany, University of Zurich, Zollikerstrasse 107, CH-8008, Switzerland. plinder@systbot.unizh.ch.

[6] Department of Botany, Faculty of Biology/Chemistry, University of Osnabrück, Barbarastrasse 11, 49069 Osnabrück, Germany. Muehlhausen@Biologie.Uni-Osnabrueck.De.

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Table 1. Classification systems for South African endemic Brassicaceae genera. Dash (—) = taxon not recognized.

	Candolle (1821)	Sonder (1846)	Prantl (1891)	Schulz (1936)	Hayek (1911)	Appel & Al-Shehbaz (1997)
Chamira Thunb.	Heliophileae	Chamireae	Thelypodieae–Chamirinae	Chamireae	Chamireae	Chamireae
Heliophila L.	Heliophileae	Heliophileae	Thelypodieae–Heliophilinae	Heliophileae	Heliophileae	Heliophileae
Thlaspeocarpa C. A. Sm.	—	—	Thelypodieae–Heliophilinae	Heliophileae	Heliophileae	Heliophileae
Cycloptychis E. Mey.	—	—	Thelypodieae–Heliophilinae	Heliophileae	Heliophileae	Heliophileae
Brachycarpaea DC.	Brachycarpeae	—	Thelypodieae–Heliophilinae	Lepidieae–Brachycarpaeinae	Heliophileae	Heliophileae
Schlechteria Bolus	—	—	—	—	Alysseae–Lunariinae	—
Silicularia Compton	—	—	—	—	—	—

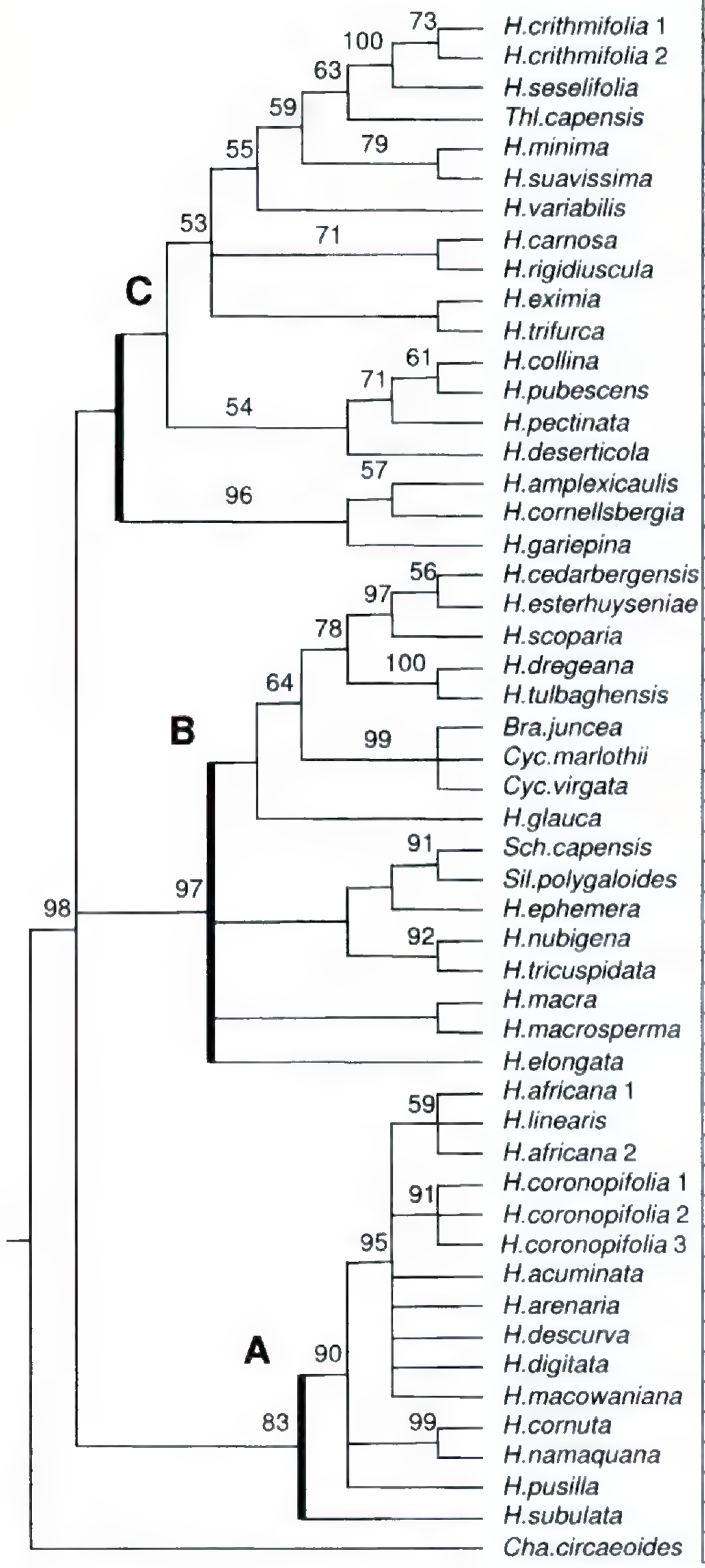
characterized the Heliophileae by having dipleco-lobal cotyledons (elongated and twice transversely folded). This uncommon cotyledonary type is also known in three Australian species of *Lepidium* L. sect. *Monoploca* (Bunge) Prantl subsect. *Diploploca* Hewson (Hewson, 1981; Mummenhoff et al., 2001), making this character homoplastic.

The Heliophileae may be regarded as the most diversified Brassicaceae lineage in every aspect of habit, flower, and fruit morphology (Table 2; compiled from Appel & Al-Shehbaz, 1997). It has flowers with enormous diversity in size ranging from the largest in the family (petals to 25 mm long in *Brachycarpaea juncea* and *Cycloptychis virgata*) to nearly the smallest (petals ca. 1.2 mm long in *Heliophila pectinata*). *Heliophila* has a wide range of flower color, including blue, a color otherwise known in Brassicaceae only in the unrelated Himalayan *Solms-laubachia* Muschl. (Al-Shehbaz & Yang, 2001). Furthermore, the flowers usually have appendages on the basal portions of petals and/or staminal filaments. Several species (e.g., *H. africana*) produce beaked fruits similar to those of the tribe Brassiceae, whereas others have siliques more than 12 cm long (e.g., *H. scoparia*) or minute silicles only about 2 mm in diameter (e.g., *H. patens*). Fruit shape is quite variable (linear, lanceolate, oblong, elliptic, ovoid, or globose), whereas fruit compression in *Heliophila* varies from latiseptate (flattened parallel to the septum) to terete, and in *Brachycarpaea* it is angustiseptate (fruit flattened at a right angle to the septum) (Figs. 1, 2). Fruits may be dehiscent (*Heliophila*), indehiscent and woody (*Silicularia*), samaroid (*Thlaspeocarpa*), or even schizocarpic and with a distinct (*Cycloptychis*) or rudimentary carpophore (*Brachycarpaea*). These fruit characters (e.g., silique versus silicle, dehiscent vs. indehiscent, latiseptate vs. angustiseptate), which are used in the separation of species and genera within Heliophileae, have been used extensively in the delimitation of tribes (see Al-Shehbaz, 1984). Within *Heliophila* one finds ephemeral to perennial herbs, shrubs, and lianas to 3 m tall (*H. scandens*). Apart from previous controversial classification systems discussed by Appel and Al-Shehbaz (1997), nothing is known about the phylogenetic relationships within the Heliophileae.

The most striking features of the CFR are the high level of endemism and the remarkable species richness. Species richness, estimated at about 9000 species in an area of 90,000 km^2 (Goldblatt & Manning, 2000), is comparable to those of the most diverse equatorial areas, and species endemism of ca. 70% is similar to that found on islands (Linder, 2003). In a recent review on the origin of the Cape

Table 2. Comparison of the six genera of the tribe Heliophileae. Data compiled from Appel and Al-Shehbaz (1997).

Character	*Cycloptychis*	*Heliophila*	*Schlechteria*	*Silicularia*	*Thlaspeocarpa*	*Brachycarpaea*
Number of species	2	73	1	1	2	1
Habit	shrubs or subshrubs	herbs, subshrubs, shrubs, or lianas	subshrubs	subshrubs	herbs	subshrubs
Appendage of staminal filament	absent	present or absent	absent	absent	present	absent
Style	long or short	long to obsolete	obsolete	short to obsolete	obsolete	short to obsolete
Ovule number	2	2 to 70	2 to 4	2	1 or 2	2
Orientation of fruiting pedicels	erect	ascending to recurved	recurved	recurved	recurved	ascending
Fruit shape	elliptic or ovate	orbicular to linear	elliptic	ovate to orbicular	elliptic to orbicular	oblate, subdidymous
Fruit compression	latiseptate	latiseptate to terete	latiseptate	latiseptate	latiseptate	angustiseptate
Fruit (dehiscence)	dehiscent	dehiscent	indehiscent	indehiscent	indehiscent	dehiscent
Carpophore	present	absent	absent	absent	absent	absent
Septum	present	present	absent	absent	absent	present
Valve texture	leathery or woody	membranous to leathery	thin leathery	± woody	thin leathery	woody
Valve sculpture	reticulate-rugose or prominently veined	smooth	smooth	reticulate rugose	with slightly raised veins	smooth to rugose
Seed shape	oval	oblong to orbicular or globose	oblong to oval	orbicular to oval	orbicular	globose
Seed wing	present or absent	present or absent	absent	absent	present	absent
Cotyledons	diplecolobal	diplecolobal	diplecolobal	diplecolobal	diplecolobal	spirally twisted



1 Section	2 Fruit type				3 Habit	4 Pedicel	5 Leaf		6 Petal	7 Anther	8 Fila-ment	9 Seed		10 Inflores-cence
	q	lat	str	deh	a	+	p	+	- / (+)	-	+	+	s	r
	q	lat	str	deh	a	+	p	+	- / (+)	-	+	+	s	r
I	q	lat	str	deh	a	-	p	+	+	-	+	+	s	r
	s	lat	str	ind	a	+	p	-	-	-	+	+	s	r
	q	lat	str	deh	a/p	+	p	+	- / (+)	-	+	+	s	r
	q	lat	mon	deh	ssa	+	e	+	-	-	-	+	s	r
III	q	lat	mon	deh	a	+	p	+	- / (+)	-	+	+	s	r
	q	lat	str	deh	ssa	+	e	+	-	-	+	+	s	r
II	q	lat	str	deh	p	+	e	+	+	-	+	+	s	r
	?	?	?	?	p	-	e	-	-	-	?	?	?	r
I	q	lat	str	deh	a	- / (+)	p	-	-	-	-	+	s	r
	q	lat	mon	deh	a	+	p	+	+	-	-	-	s	r
VI	q	lat	mon	deh	a	+	p	+	-	-	-	-	s	r
I	q	lat	mon	deh	a	+	p	+	-	-	-	-	s	r
	q	lat	str	deh	a	-	p	-	- / (+)	-	- / +	+	s	r
III	q	lat	mon	deh	a	-	e	-	+	-	+	+	s	r
	s	inf	str	deh	a	-	e	-	+	-	+	+	s	r
	q	lat	mon	deh	a	-	e	-	+	-	-	+	s	r
	q	lat	str	deh	ss	+	e	+	-	+	-	-	p	i
	q	ter	str	deh	ss	+	e	+	-	+		-	p	i
II	q	lat	str	deh	s	+	e	+	-	+	-	+	p	i
II	q	ter	mon	deh	ss	+	e	+	-	+	-	-	p	i
	q	ter	mon	deh	ss	+	e	+	-	+	-	-	p	i
	s	ang	str	deh	ss	+	e	-	-	+	-	-	s	r
	s	lat	str	deh	ss	-	e	-	-	+	-	-	s	r
	s	lat	str	deh	ss	-	e	-	-	+	-	-	s	r
II	q	lat	str	deh	ssa	-	e	-	-	+	-	-	s	r
	s	lat	str	ind	ss	+	e	-	-	+	-	-	s	r
	s	lat	str	ind	ssa	+	e	-	-	+	-	-	s	r
	s	inf	str	deh	a	+	e	-	-	+	-	-	s	r
	s/q	lat	str	deh	ss	-	e	-	-	+	-	-	s	r
	q	lat	str	deh	ss	+	e	+	-	+	-	-	s	r
	q	lat	str	deh	ssa	-	e	+	-	-	-	-	s	r
IV	q	lat	str	deh	ss	+	e	+	-	+	-	-	s	r
II	q	lat	str	deh	ssa	+	e	+	-	-	-	-	s	r
I	q	lat/ter	str	deh	a	-	e	-	+	-	+	-	s	r
I	q	lat	str	deh	p	-	e	-	+	-	+	+	s	r
I	q	lat/ter	str	deh	a	-	e	-	+	-	+	-	s	r
VI	q	lat	mon	deh	a	- / (+)	e	- / (+)	+	-	+	-	s	r
VI	q	lat	mon	deh	a	- / (+)	e	- / (+)	+	-	+	-	s	r
VI	q	lat	mon	deh	a	- / (+)	e	- / (+)	+		+		s	r
VI	q	lat	mon	deh	a	-	e	-	- / +	-	+	-	s	r
V	q	lat	mon	deh	a	-	p	-	+	-	+	-	s	r
	q	lat	str	deh	a	-	e	+	+	-	+	-	s	r
	q	ter	str	deh	a	-	p	-	+	-	+		s	r
	q	lat	mon	deh	a	- / (+)	p	+	(-) / +	-	+		s	r
II	q	lat	mon	deh	s	-	e	-	+	-	+	-	s	r
	q	lat	str	deh	a	-	e	- / (+)	- / (+)	-	- / (+)	+	s	r
III	q	lat	mon	deh	a	-	e	-	- / (+)	-	+	-	s	r
II	q	lat	str	deh	a/p/ss	+	e	+	-	-	-	-	s	r
	q	lat/ter	str	deh	a	-	e	-	-		-	-	s	r

Figure 1. Strict consensus ITS tree with the distribution of morphological data in *Heliophila* and related genera. *Cleome spinosa* (Cleomaceae), *Aethionema saxatile*, *Alliaria petiolata*, *Rorippa amphibia*, and *Cardamine matthioli* (Brassicaceae) served as the outgroup. The consensus tree is based on 14,560 equally parsimonious reconstructions found after heuristic search; jackknife support > 50% (10,000 replicates) are indicated at the branches. Taxon abbreviation: *H.* = *Heliophila*, *Thl.* = *Thlaspeocarpa*, *Bra.* = *Brachycarpaea*, *Cyc.* = *Cycloptychis*, *Sch.* = *Schlechteria*, *Sil.* = *Silicularia*, *Cha.* = *Chamira*.
[1] **Sectional classification of Sonder (1846)**: I = *Orthoselis* subsection 1: herbaceous species, II = *Orthoselis* subsection 2: shrubby species, III = *Ormiscus*, IV = *Lanceolaria*, V = *Pachystylum*, VI = *Leptormus*. *Heliophila* species not characterized by Roman numerals were not recognized by Sonder (1846) or they represent other genera. [2] **Fruit types: relative fruit length**: q = silique, s = silicle; **orientation and degree of the fruit compression**: lat = latiseptate, ang = angustiseptate, ter = terete, inf. = inflated; **fruit margin**: mon = moniliform (fruits deeply constricted between the seeds), str = fruits with straight margins; **fruit opening**: deh = dehiscent, ind = indehiscent. [3] **Habit:** a = annual herb, p = perennial herb, s = shrub, ss = subshrub, ssa = subshrub, but annual shoots arising from a woody crown. [4] **Pedicel:** + = with two small bracts, − = without two small bracts. [5] **Leaf:** p = pinnately divided, e = entire; − = leaves exstipulate, + = leaves subtended by two minute stipules. [6] **Petal:** − = without basal appendages, + = with basal appendages. [7] **Anther:** + = presence of apicula, − = apicula absent. [8] **Filament:** + = with basal appendages, − = without basal appendages. [9] **Seed:** - = wingless or with a very narrow margin, + = distinct wing; p = papillate, s = smooth. [10] **Inflorescence:** r = raceme, i = intercalary inflorescence. Data compiled from Marais (1970), Bean (1990), and Goldblatt and Manning (2000) and the authors' studies of specimens at MO.

flora, Linder (2003) suggested that the high level of endemism might be the consequence of ecological and geographical isolation of the CFR. He also suggested that the species richness might be the consequence of radiation that started between 18 and 8 million years ago, which might be accounted for by the diverse limitations to gene flow (e.g., dissected landscapes, pollinator specialization), as well as by a climatically and topographically complex environment (e.g., altitudinal variation, soil types) allowing numerous niches and resulting in highly fragmented distribution ranges.

Studies are needed to provide (i) phylogenetic data demonstrating the monophyly of diversifying lineages in the CFR, (ii) more molecular clock estimates to accurately date the radiation, and (iii) species-level phylogenies to detect sister-species relationships to study speciation. The current study addresses these needs by providing a robust phylogeny of the tribe Heliophileae based on the nuclear ITS region of 55 of its 80 species. We used nonparametric rate smoothing (NPRS) of Sanderson (1997), as well as a "forced" (global) clock approach to date the diversification of Heliophileae by implementing fossil data and published calibration points (Wikström et al., 2001) and a range of published rDNA ITS substitution rates. In addition, the pattern of species distribution in relation to their ecology and phylogeny was investigated in an attempt to get insights into speciation mode in this lineage.

Material and Methods

Morphology

All species of *Brachycarpaea, Cycloptychis, Heliophila, Silicularia, Schlechteria,* and *Thlaspeocarpa* have been critically evaluated morphologically. The characters studied, all considered to be taxonomically important (see Marais, 1970), include habit; presence vs. absence of staminal appendages; ovule number per ovary; orientation of fruiting pedicels; fruit shape, dehiscence, compression, presence vs. absence of carpophore, development of the septum, valve texture, and valve sculpture; seed shape and presence vs. absence of wing; and cotyledonary type. These are listed in Table 2 and Figure 1 and need no further details.

DNA Extraction, Gene Amplification, and Sequencing

Plant material, locality information, voucher details, and GenBank accession numbers are given in Appendix 1. *Cleome spinosa* (Cleomaceae), *Aethionema saxatile, Alliaria petiolata, Rorippa amphibia,* and *Cardamine matthioli* were chosen as outgroups on the basis of previous molecular phylogenetic studies (Koch et al., 2001). Methods for DNA extraction, PCR amplification of the rDNA ITS and cpDNA *trn*L-F regions, BigDye terminator labeled sequencing, sequence assembly and alignment are described in Bowman et al. (1999) and Mummenhoff et al. (2001, 2004).

Data Analysis

The aligned sequences were subjected to both parsimony and Bayesian analysis, using PAUP*4.0b10 (PPC/Altivec) and MrBayes 3 (Ronquist & Huelsenbeck, 2003) implemented on a Macintosh G4 computer. Jackknife analysis was carried out using PAUP* with settings so as to emulate Parsimony Jackknifer (Farris et al., 1996): percentage of characters deleted in each replicate = 37, "fast" stepwise addition, and "Jac" re-sampling method. Heuristic searches involved TBR branch swapping, MULPARS, and collapse branches when maximum length is zero. Starting trees were generated by 1000 cycles of random addition sequence holding 3 trees at each step, and keeping no more than 1000 trees > length 904 steps. Trees resulting from this search were then used as starting trees in a subsequent search during which they were swapped to completion as far as possible.

Bayesian analysis was performed on the ITS alignment using settings derived from ModelTest analysis (Posada & Crandall, 1998): the maximum likelihood model employed 6 substitution types ("nst = 6") and rate variation across sites was modeled using a gamma distribution (rates = "gamma"), while invariant sites were also assumed. The Markov chain Monte Carlo search was run with 4 chains, one of which "cold," for 1,000,000 generations, with trees being sampled every 100 generations. After discarding the first 10% of trees as "burnin," Bayesian search results were summarized by 50% majority rule consensus and the posterior probability values ("clade credibilities") are indicated at the branches (Fig. 2).

Likelihood ratio testing was performed using the Bayesian 50% majority rule consensus tree in order to check for a molecular clock. An ultrametric tree was then produced from the Bayesian consensus tree using both NPRS as implemented in the program "r8s" version 1.06 (beta) described by Sanderson (1997), as well as by "forcing" a clock in PAUP*. The Heliophileae ITS tree with branch lengths in six decimals was saved and input in r8s, in which the following branch length format settings

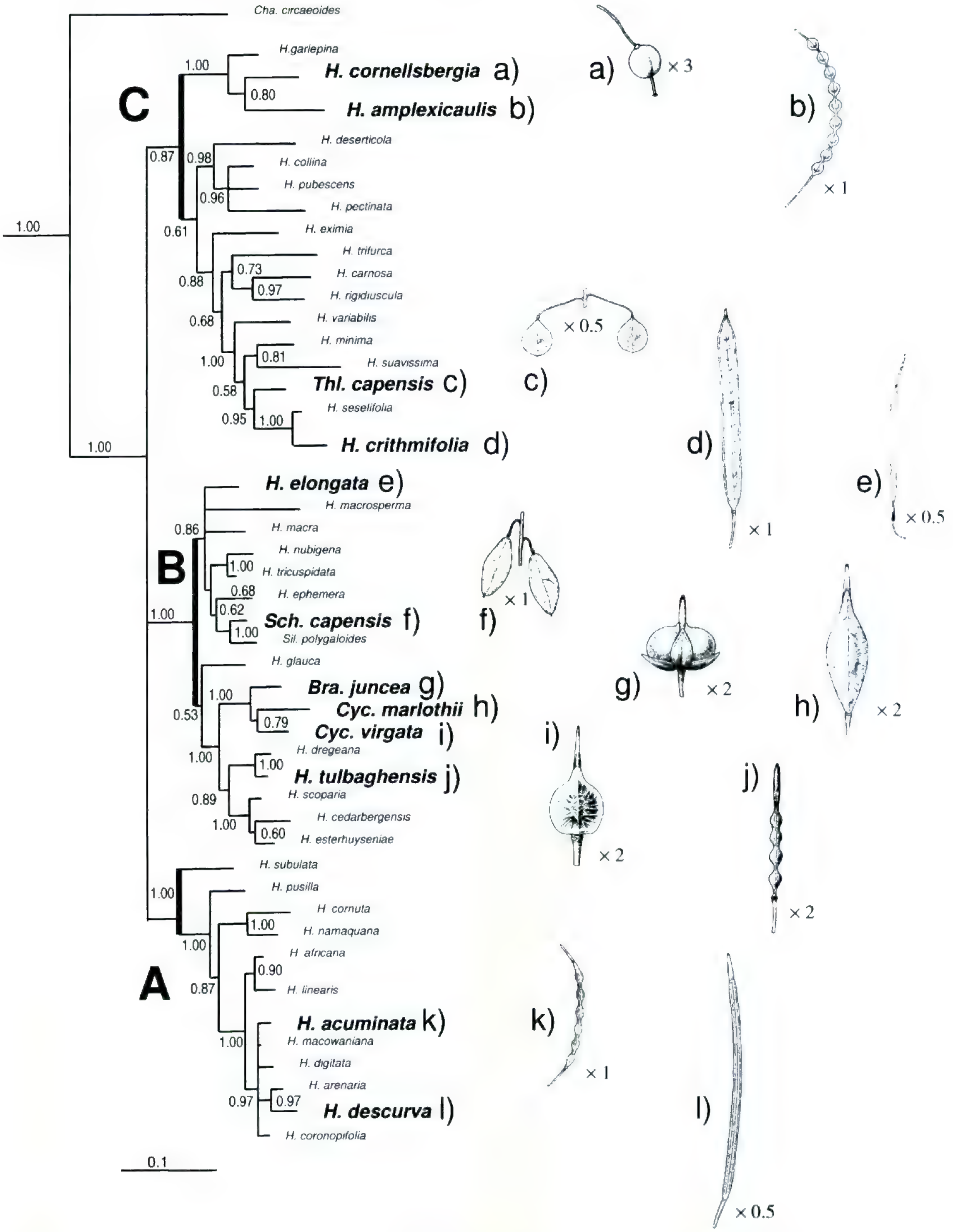


Figure 2. Bayesian consensus tree with mean branch length and a posteriori probabilities, and the distribution of fruit types among the main clades of *Heliophila* s.l. Taxon abbreviation follows Figure 1. *Cleome spinosa* (Cleomaceae), *Aethionema saxatile*, *Alliaria petiolata*, *Rorippa amphibia*, and *Cardamine matthioli* (Brassicaceae) served as the outgroup. Illustrated species written in larger bold font.

were used: "length = persite, nsites = 498, ultrametric = no, round = yes"; divergence times of other than the fixed node (see below) were estimated using the settings: "method = NPRS, algorithm = POWELL," and "set num_time_guesses = 10" in order to ensure optimal exploration of solution space.

In order to estimate error around node ages, we performed 100 replications of constrained jackknife analysis of the data matrix, saving each tree under the topological constraints of the Bayesian consensus tree. In this way, identical topology trees are produced with variation in branch lengths reflecting "substitutional noise" as picked up by the re-sampling procedure. All hundred trees were then analyzed in r8s with respect to their A, B, and C nodes, using the settings above. Age estimates around these nodes were summarized using the "profile" command.

In addition, we prepared a "forced (global) clock" tree in PAUP*. In this approach an ultrametric tree is produced by assuming overall clock-like behavior of the data, under otherwise the same likelihood model as the one arrived at in the Bayesian analysis described above. Forced clock trees were made in- and excluding the outgroup *Cleome spinosa*.

As an alternative to the calibration using the dates from Wikström et al. (2001), we also calibrated our ultrametric trees by applying a range of published rDNA ITS substitution rates. We took the rates published for *Dendroseris* D. Don (Asteraceae) from Sang et al. (1994), i.e., 3.9×10^{-9} subst./site/yr, and *Soldanella* L. (Primulaceae) from Zhang et al. (2001), i.e., 8.3×10^{-9} subst./site/yr, to represent the currently known range of substitution rate for this region in angiosperm eudicots. Ultrametric tree node height H is the result of accumulated substitutions per site along two evolutionary lines; therefore height = substitution rate $r \times$ twice divergence time T, and T can be calculated as $H/2r$. Rate calibration was performed in TreeEdit v. 1.0a10 (Rambaut & Charlston, 2001) by dividing the ultrametric node heights by twice the substitution rate, and multiplying by the number of sites used (n = 498) in order to arrive at node heights in millions of years.

We used fruit fossil data of *Rorippa* Scop. (2.5–5 million years old; Mai, 1995) to constrain the clade containing *Rorippa* and *Cardamine* L. at 2.5–5 mya minimally. These genera have been shown to be sister taxa in several phylogenetic studies (e.g., Mummenhoff et al., 2001, 2004).

ECOLOGICAL OPTIMIZATIONS

We followed the species-level taxonomy of Marais (1970) because it is the only comprehensive account of the Heliophileae. However, he did use a rather broad species concept and recognized many infraspecific taxa occupying ecologically heterogeneous habitats. The ecological attributes of the species, and their distribution ranges, were taken primarily from Marais (1970). In addition, the herbarium holdings of BOL and PRE were surveyed for collection data, though their identities were not verified because most of them were studied by Marais and are well curated. Altitudinal data were checked against the ranges in Germishuizen and Meyer (2003) and Goldblatt and Manning (2000).

Species were scored for the following four environmental parameters:

1. Distribution ranges (Roggeveld, Drakensberg, Eastern Cape, Southern Cape, Swartruggens, central Cape mountains, Cedarberg-Nieuwoudtville, Kamiesberg, Gordonia, Richtersveld, Namib). These ranges follow a combination of topographical features of southern Africa that often provide natural boundaries to species distribution, and this theme is used in combination with actual climatic zones (see Fig. 3).

2. Vegetation type (woodland, forest, grassland, Karoo, thicket, Namaqua Broken Veld, succulent Karoo, Renosterveld, Strandveld, Fynbos). These types are largely structural rather than floristic. Karoo refers to the shrubby to grassy semi-arid summer-rainfall vegetation of the central uplands of southern Africa, whereas succulent Karoo is a very succulent shrubby winter-rainfall semidesert vegetation (Rutherford & Westfall, 1986). Namaqua Broken Veld is a taller shrubland characteristic of the granitic escarpment of Namaqualand (Acocks, 1975). Renosterveld, strandveld, and fynbos are typical vegetation types of the Cape Floristic Region. The first is a widespread shrubland on richer soils dominated by *Elytropappus rhinocerotis* (L. f.) Less. (Asteraceae). Strandveld is a non-pyrophytic woody shrubland of coastal dunes, and fynbos is the typical pyrophytic heath vegetation of oligotrophic soils dominated by Restionaceae, Proteaceae, and Ericaceae.

3. Bedrock/substrate types (sandstone, shale, granite, coastal sand, acidic sand, limestone, Karoo shale). These categories represent the substrate of a general area, rather than a specific microhabitat, and as such can be inferred from geological maps. Sandstone, shale, limestone, coastal sand, and acidic sand are the major substrate types of the Cape Floristic Region. Karoo shale refers to the

Figure 3. Distribution areas of *Heliophila* species and related genera in outlines. The distributional categories follow a combination of the topographical features of southern Africa, which often provide natural boundaries to distribution ranges, used in combination with actual distributions and zones of climatic change (see Goldblatt & Manning, 2000; Cowling & Heijnis, 2001).

fine-grained sedimentary rock that is widespread throughout the Karoo basin and also forms the pediments of the Drakensberg. Much of the Namaqualand escarpment is granitic.

4. Soil type (stony-gravel, gravel, sand, calcrete, loam, boulders, clay). This indicates the substrate at the microhabitat scale, and is recorded largely from herbarium notes.

The environmental attributes of the internal cladogram nodes were inferred using DIVA optimization (Ronquist, 1997). This optimization was developed to track changes in the distributions of clades, assuming that vicariance and sympatric speciation were the "normal" situation, by attaching a cost to dispersal, but not to sympatric speciation or vicariance. This method does not enforce monomorphy at internal nodes, and it allows ancestors to remain polymorphic for individual attributes. As such it is the ideal approach for inferring the evolutionary history of environmental attributes (Linder & Hardy, 2005; Hardy & Linder, 2005). It is implemented in the software DIVA (Ronquist, 1996). In the biogeographical analysis the number of possible results obtained by DIVA was very large. Therefore, a maximum of four areas were assigned to any ancestral node reconstruction. This impacted the reconstruction of the basal but not the more terminal nodes. In order to use DIVA, a fully resolved tree was needed, and one of the maximally parsimonious trees was arbitrarily chosen for this analysis. The environmental attribute information for some species was incomplete; in these cases the species were scored the same as their sister species.

Results

Phylogenetic Analysis

The ITS alignment, including the outgroups (*Cleome spinosa* (Cleomaceae), *Aethionema saxatile*, *Aliaria petiolata*, *Rorippa amphibia*, and *Cardamine matthioli* (Brassicaceae)), contained 57 taxa and 473 characters of which 195 were parsimony informative. Using the above-mentioned settings, parsimony searches yielded 14,560 MPTs 904 steps long (CI = 0.52, RI = 0.69) of which the strict consensus is shown in Figure 1. In the Bayesian analysis and after the MCMC had finished, 1000 out of the 10,000 trees sampled were discarded as burnin "trees." Model parameter values had con-

Table 3. Date estimates of the Heliophileae clade and its comprising subclades A, B, and C based on different approaches; numbers indicate millions of years. See text for further details.

Calibration	Heliophileae	Node A	Node B	Node C
Wikström et al.[1]				
NPRS[2]	4.2/4.6	3.4/3.7	2.9/3.3	3.9/4.3
NPRS jackknife[3]	3.7–5.4	2.8–4.5	2.2–3.9	n.a.
Forced clock[4]	1.9	1.3	1.0	1.7
rDNA ITS rates[5]				
non-ultrametric distances	2.7–5.8	1.1–2.3	1.5–3.2	2.2–3.8
Forced clock[4]	2.3–4.9	1.6–3.3	1.3–2.7	2.1–4.4

[1] The Brassica/Cleome clade was dated 22 mya (from Wikström et al., 2001).
[2] Tree made ultrametric using NPRS; additional calibration by constraining the Rorippa/Cardamine clade to be minimally 2.5/5.0 mya.
[3] Estimated on jackknife re-sampled branch lengths under NPRS.
[4] Tree made ultrametric assuming a global clock.
[5] (3.9–8.3) × 10^{-9} subst./site/year (from Sang et al., 1994; Zhang et al., 2001).

verged at TL = 3.15 (± 2.67), r(C↔T) = 5.15 (±0.82), r(C↔G) = 0.74 (± 0.03), r(A↔T) = 2.22 (± 0.21), r(A↔G) = 2.98 (± 0.31), r(A↔C) = 1.42 (± 0.11), pi(A) = 0.27, pi(C) = 0.23, pi(G) = 0.22, pi(T) = 0.29, α = 1.08, and pinvar = 0.12. Parsimony and Bayesian tree topologies were largely congruent.

The cpDNA *trn*L intron region data set included 370 base pairs, of which 57 were variable characters and only 13 were phylogenetically informative. Due to the lack of informative characters, both parsimony and Bayesian analysis of this data set resulted in a poorly resolved tree topology. Eight cpDNA lineages were found that were all present (except two species) in the ITS toplogy as well. However, their relationships and the main lineages A, B, and C could not be resolved. Thus, the discussion hereafter is based on the ITS data only.

In all phylogenetic trees, one robust main clade with three sublineages A through C is recognized (Figs. 1, 2). These three clades form a trichotomy in the strict consensus tree and the Bayesian tree, and they comprise all *Heliophila* species along with the genera *Thlaspeocarpa* (clade C), *Brachycarpaea*, *Cycloptychis*, *Schlechteria*, and *Silicularia* (clade B). Within clade B, *Brachycarpaea juncea*, *Cycloptychis marlothii*, and *C. virgata* form a well-supported monophyletic group (jackknife support 99%), whereas *Schlechteria capensis* and *Silicularia polygaloides* form the other. *Chamira* is a sister to the main lineage, referred to hereafter as *Heliophila* s.l.

TIME ESTIMATES

The Bayesian tree was tested for clocklike behavior of the data using likelihood ratio testing. With all model parameters estimated and excluding some of the outgroup taxa, i.e., *Cleome spinosa* and *Aethionema* R. Br., a molecular clock was rejected ($P < 0.01$); therefore, the ingroup tree was made ultrametric using the NPRS method as implemented in r8s, as well as by applying a global clock in PAUP* ("forced clock," see below). Node ages were then estimated in the following ways: the age of the entire tree including *Cleome spinosa* and *Aethionema* was fixed at 22 (± 2) mya, as this is the age estimated by Wikström et al. (2001) for their *rbc*L-based Brassica/Cleome clade. The dates in Wikström et al. (2001) may be severe underestimates of clade ages, possibly due to the "thin" taxon sampling in that study (Wikström et al., 2003). Therefore, actual dates obtained here for the *Heliophila* ITS tree may be too young as well, although it is not clear by how much. Moreover, as no further outgroup ITS sequences could be aligned to the *Heliophila* matrix, the only option was to fix the entire tree rather than apply a maximum constraint. In addition, we simultaneously applied a minimum age constraint of 2.5–5 mya for the clade containing *Rorippa amphibia* and *Cardamine matthioli*, as this corresponds to the age of *Rorippa* fruit fossils (range 2.5–5 mya; Mai, 1995). The r8s analysis described above estimated the age of the Heliophileae clade to be 4.2–4.6 mya, whereas the constrained jackknife analyses yielded a range of 3.7–5.4 mya for the same node, and subclades A and B were estimated to be 2.8–4.5 and 2.2–3.9 mya, respectively. The confidence analysis for clade C could not be completed because the clade was not present in a large proportion of jackknife trees (for all dating results, see Table 3).

The "forced clock" approach yielded ultrametric trees with significantly shorter branches within the Heliophileae s.l. lineage than those obtained with NPRS. This phenomenon has been observed before (Barraclough & Reeves, 2005; Linder & Hardy, 2004; Linder et al., 2005), and it is not fully understood at the moment. In order to assess the possible influence of the relatively long *Cleome spinosa*-ingroup branch, we repeated the forced clock analysis excluding this outgroup to prevent < 0.5% increase of branch length in the ingroup (not shown). "Forced clock" ultrametric tree was then analyzed in TreeEdit using the "scale tree" option, scaling the total "node height" to 22 mya. This yielded 1.9 mya for the Heliophileae clade and between 1.0 and 1.7 mya for the main three subclades A, B, and C.

An application of a range of published rDNA ITS substitution rates on the forced clock ultrametric branch lengths (see above) yielded the age 2.3–4.9 mya for the Heliophileae clade. An age estimate of 2.7–5.8 mya for the Heliophileae clade resulted from the application of substitution rates to the (non-ultrametric) GTR+I+Γ distances observed among the rDNA ITS sequences. This estimate is in agreement with the "ultrametric" estimates (maximum distance $D = 22.43\%$ between *Cycloptychis marlothii* and *Heliophila suavissima*; D = substitution rate $r \times$ number of sites $n \times$ twice divergence time T, and therefore T can be calculated as $D/2rn$; using either the 3.9×10^{-9} or 8.3×10^{-9} subst./site/yr for rDNA ITS rate, and with n being 498, this approach yields an age estimate for the tribe at 2.7–5.8 mya).

ECOLOGICAL OPTIMIZATIONS IN *HELIOPHILA*

The optimization to the basal node or even basal three nodes using DIVA is generally poorly resolved, as no sensible outgroup could be used. Therefore, an interpretation of the basal nodes was avoided in this study, and instead we report the situation within the three main clades.

The distributional optimization (Fig. 4) shows that clades A and B are centered in the Cedarberg–Nieuwoudtville area, with *H. cornuta* being the only widespread species. Several species are found further to the east in the central southern Cape mountains, and this is especially evident in clade B. Clade C is centered in the Richtersveld, with outliers reaching south to the Roggeveld, and east to the Drakensberg (*H. carnosa–H. rigidiuscula*). The soils optimization (Fig. 5) shows that sandy soils are generally preferred, especially in clades A and C. Clade B is remarkable for its preference for boulders and ledges, and occasionally for gravelly soils. Clade B is almost entirely perennial, with a single annual species; clades A and C are largely annual, but perennial lineages evolved seven times (Fig. 6).

The vegetation type optimization (Fig. 7) shows clades A and B centered in fynbos, with outliers in renosterveld, strandveld, and also the surrounding arid vegetation types. Clade C is more common in Karooid vegetation, but with a wider range of outliers than clades A and B — these include grassland, succulent karoo, fynbos, renosterveld, Namaqua Broken Veld, among others. The rock types (Fig. 8) are simple, with clades A and B primarily found on sandstone (with outliers on granite, shale, coastal and acidic sand). Clade C is primarily found on Karoo shale.

DISCUSSION

TAXONOMIC CONSIDERATIONS

Tribal level

Phylogenetic relationships within the Brassicaceae have been a source of considerable controversy, and the most frequent problems are associated with the tribal classification and delimitation of genera, including some larger ones such as *Alyssum* L., *Arabis* L., *Brassica* L., *Draba* L., *Heliophila*, *Lepidium*, and *Sisymbrium* L. (Koch et al., 2003, and references therein). These problems are mostly the result of a heavy reliance on potentially homoplastic fruit characters (Koch et al., 2003).

The Heliophileae were considered by Appel and Al-Shehbaz (1997) as a natural, well-defined tribe based on a single synapomorphy, diplecolobal cotyledons. One of its genera, *Brachycarpaea*, has spirally coiled cotyledons, a feature interpreted by them as derived from diplecolobal ones. The rather unexpected occurrence of diplecolobal cotyledons in three Australian species of *Lepidium* sect. *Monoploca* subsect. *Diploploca* (Hewson, 1981) was shown by Mummenhoff (unpublished) to have evolved independently from that of the Heliophileae. The monotypic *Chamira* has persistent, twice longitudinally folded cotyledons that act as the major photosynthetic organ. These features were used by Appel and Al-Shehbaz (1997) to maintain the genus in a unigeneric tribe, Chamireae. The present ITS study supports the recognition of the Heliophileae as a monophyletic group, with *Chamira* as sister, underlining the potential broad-scale phylogenetic utility of molecular markers in the Brassicaceae. The evaluation of Chamireae as a distinct

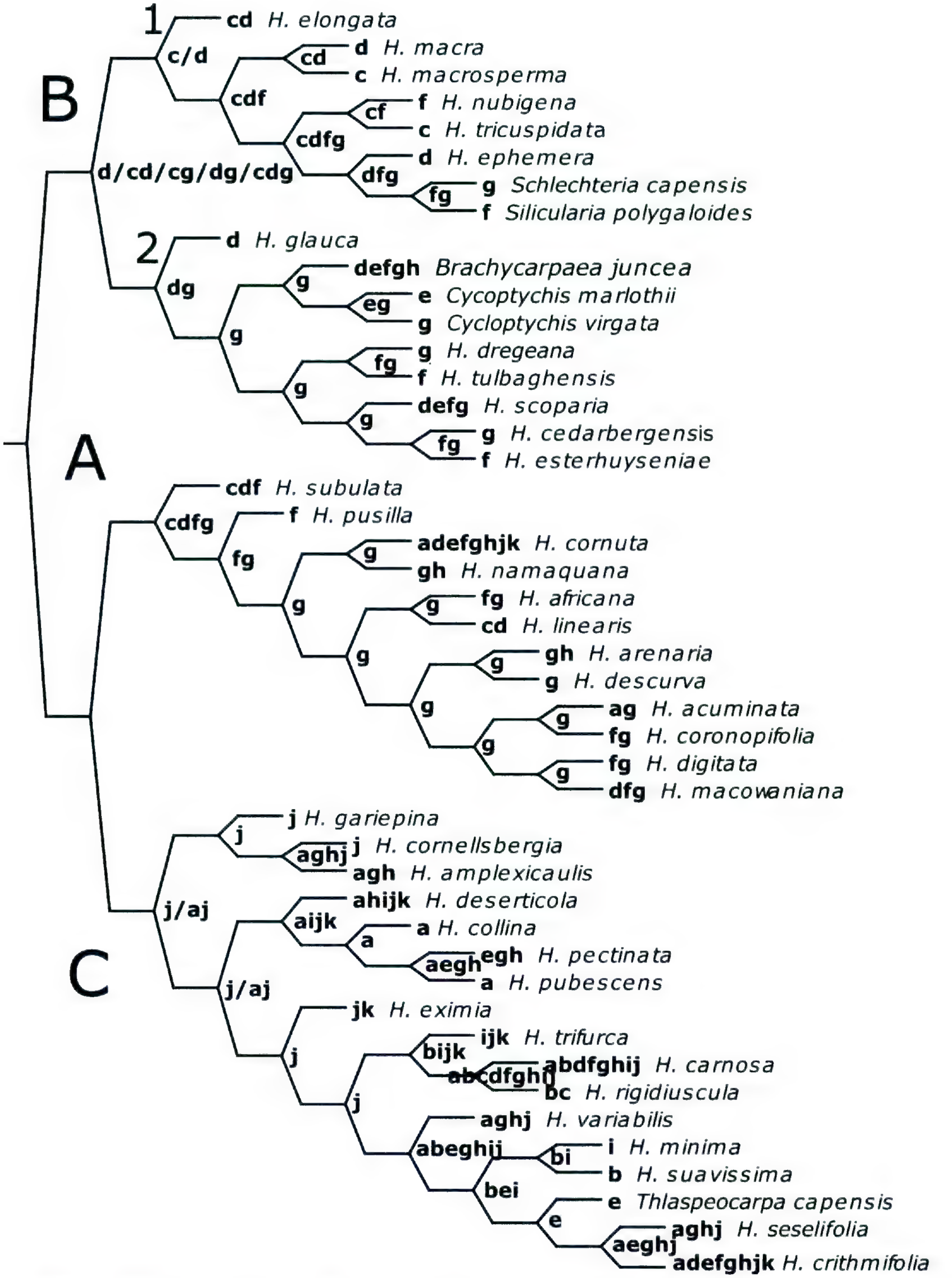


Figure 4. Distribution optimizations. Where many possible optimizations were indicated at an internal node, only the most widespread (that includes all areas of the other, more limited optimizations) is indicated. This is the most conservative possible route. Where only two, different optimizations are indicated, they are separated by a backslash. Area codes are: a—Roggeveld; b—Drakensberg; c—Eastern Cape; d—Southern Cape; e—Swartruggens; f—central Cape mountains; g—Cedarberg-Nieuwoudtville; h—Kamiesberg; i—Gordonia; j—Richtersveld; k—Namib. H. = *Heliophila*.

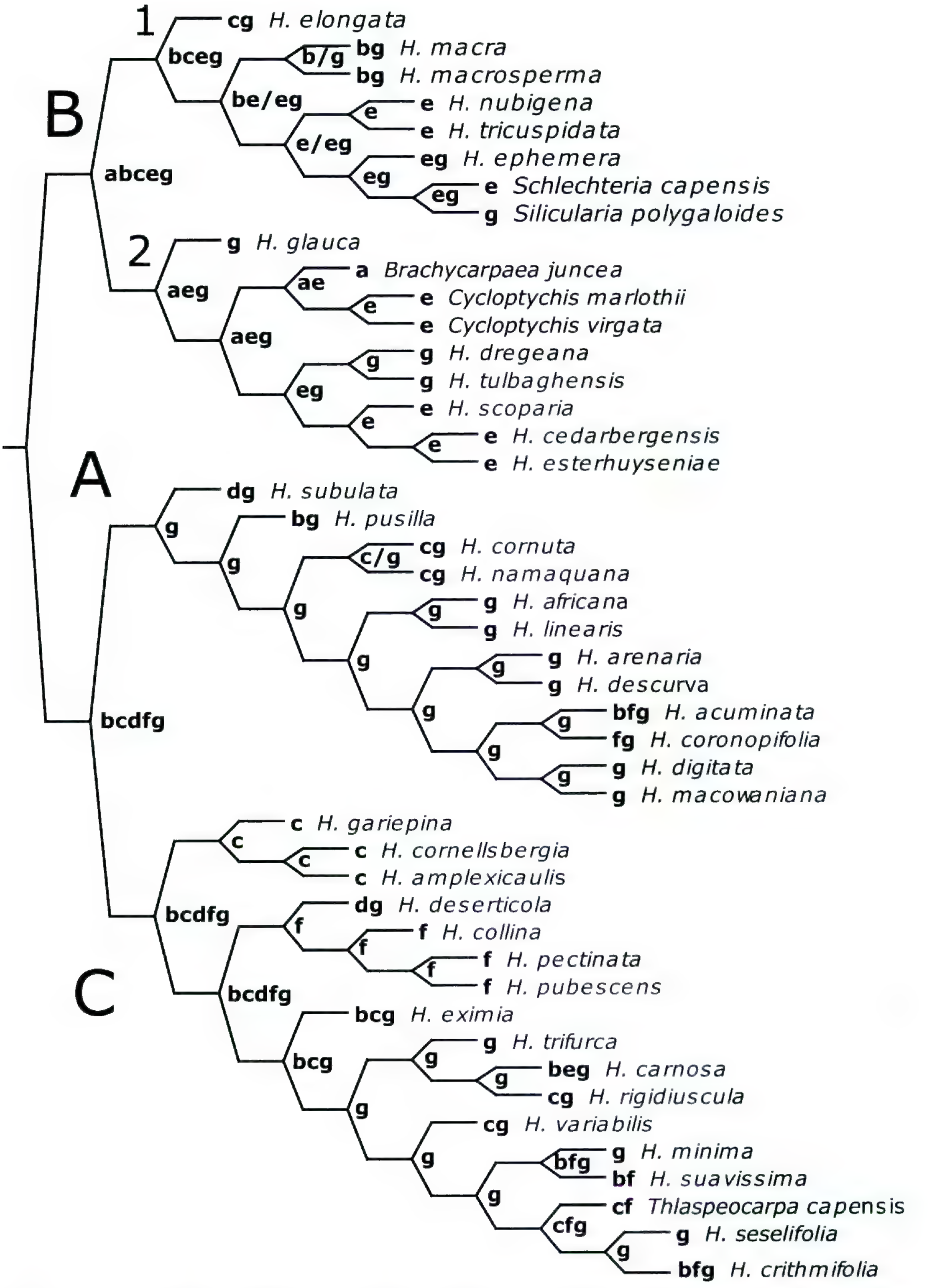


Figure 5. Soil optimizations. Where many possible optimizations were indicated at an internal node, only the most polymorphic (that includes all soils of the other, more limited optimizations) is indicated. This is the most conservative possible route. Where only two, different optimizations are indicated, they are separated by a backslash. Soils codes are: a—stony-gravel; b—gravel; c—loam; d—calcrete; e—boulders; f—clay; g—sand. H. = *Heliophila*.

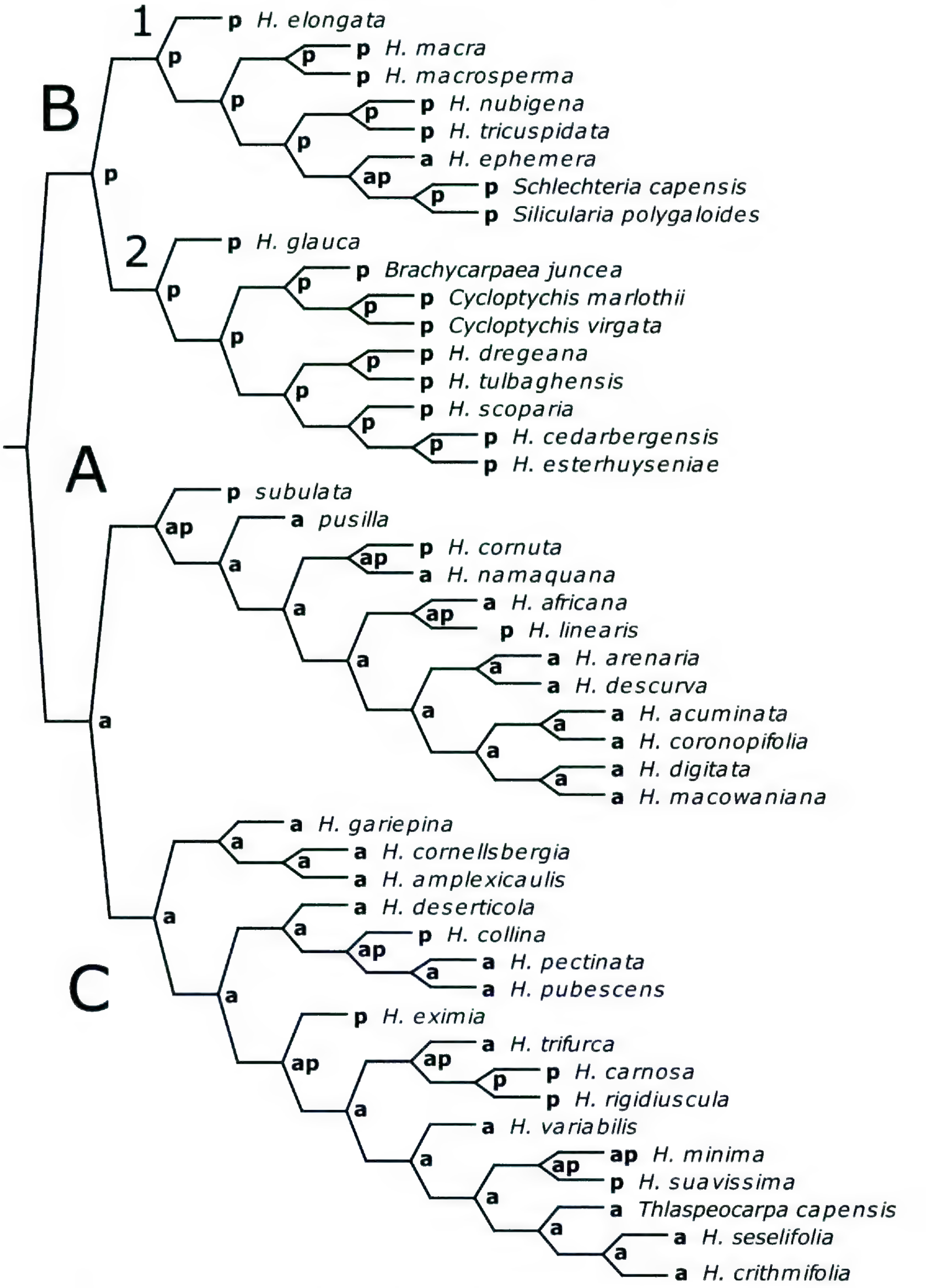


Figure 6. Habit optimizations. Habit codes are: a—annual; p—perennial. H. = *Heliophila*.

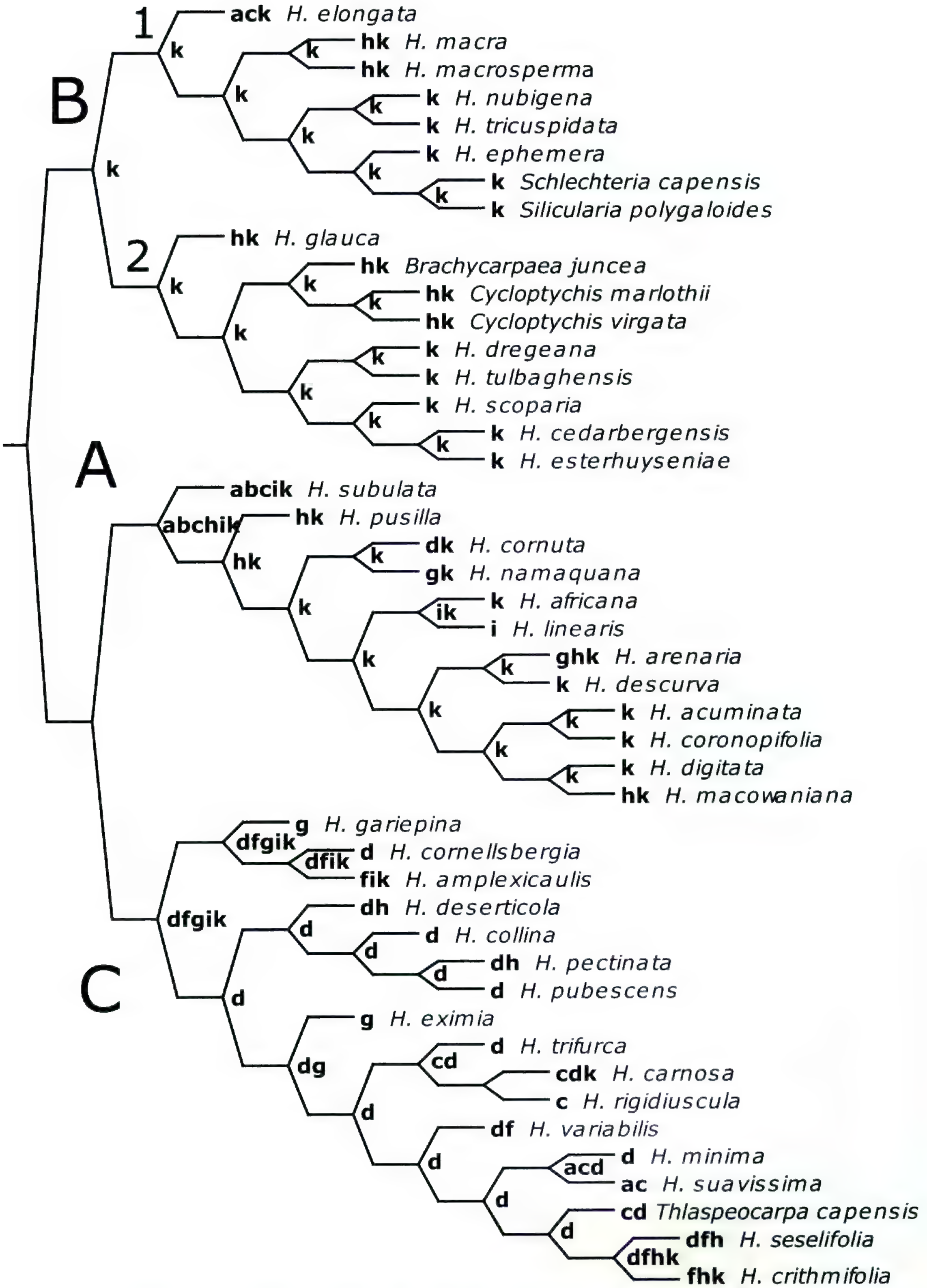


Figure 7. Vegetation optimizations. Where many possible optimizations were indicated at an internal node, only the most polymorphic (that includes all vegetation types of the other, more limited optimizations) is indicated. This is the most conservative possible route. Where only two, different optimizations are indicated, they are separated by a backslash. Vegetation codes are: a—woodland; b—forest; c—grassland; d—Karoo shrublands; f—Namaqua Broken Veld; g—succulent Karoo; h—Renosterveld; i–Strandveld; k—Fynbos. H. = *Heliophila*.

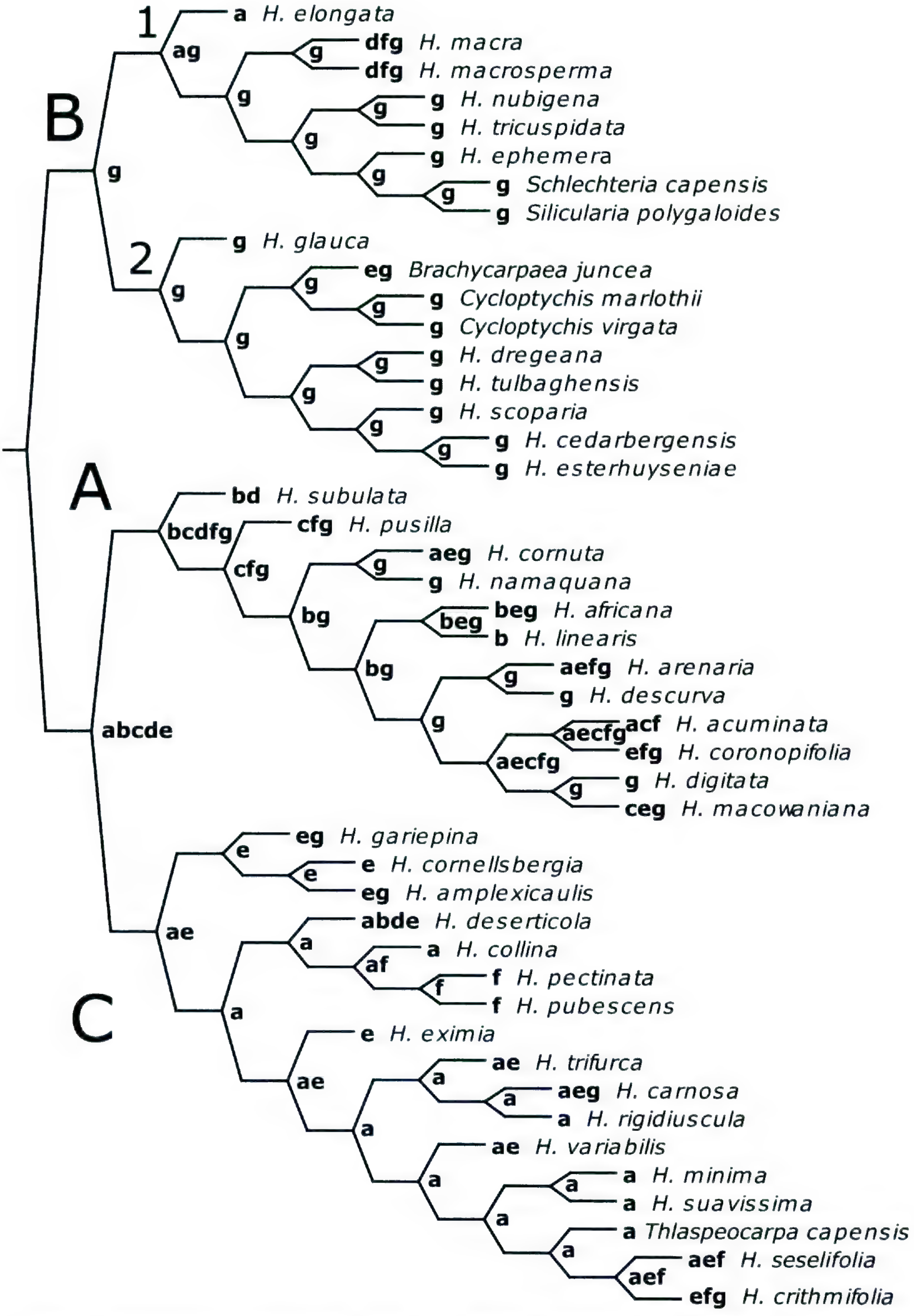


Figure 8. Bedrock/substrate optimizations. Where many possible optimizations were indicated at an internal node, only the most polymorphic (that includes all bedrock types of the other, more limited optimizations) is indicated. This is the most conservative possible route. Where only two, different optimizations are indicated, they are separated by a backslash. Bedrock codes are: a—Karoo Shale; b—coastal sand; c—acidic sand; d—limestone; e—granite; f—shale; g—sandstone. H. = *Heliophila*.

tribe must await a comprehensive family-wide phylogenetic analysis.

Generic limits within Heliophileae

Large genera of Brassicaceae (e.g., *Lepidium*) are usually well characterized by distinct fruit types but exhibit considerable variation in habit (Mummenhoff et al., 2001). By contrast, *Heliophila* s.l. shows both extreme variation in habit and striking multitude of fruit shapes (Figs. 1, 2, Table 2). As many as nine smaller genera have been segregated from *Heliophila* (for synonymy, see Marais, 1970), all of which represent morphological extremes connected by intermediates in almost every conceivable character combination (Appel & Al-Shehbaz, 1997). Although different classification schemes of the Heliophileae have been proposed, the tribal disposition of and systematic relationships among component genera are unknown, and no phylogenetic concept has been put forward so far. All five smaller genera assigned by Appel and Al-Shehbaz (1997) to this tribe (Table 1) are well nested in two of the three clades of *Heliophila* in the molecular trees (Figs. 1, 2). *Thlaspeocarpa capensis* is included in clade C, whereas *Brachycarpaea juncea* together with the two *Cycloptychis* species, and *Silicularia polygaloides* along with *Schlechteria capensis* form two monophyletic groups within clade B, respectively. The phylogenetic position of these taxa in the molecular tree is also supported morphologically. The two species of *Cycloptychis* clearly form a monophyletic assemblage characterized by the presence of a carpophore, a feature not found elsewhere in the Heliophileae. *Cycloptychis* is easily distinguished from *Heliophila* by its schizocarpic, erect, appressed fruits with carpophores, and sculptured, thick, leathery or woody fruit valves (Table 2). *Brachycarpaea* is well defined by its angustiseptate fruits and spirally coiled cotyledons, but it strikingly resembles *Cycloptychis* in habit, flower size and morphology, schizocarpic fruits (though with a rudimentary carpophore) with one-seeded mericarps, apiculate anthers, and smooth seeds. Therefore, these remarkable morphological similarities are in complete agreement with the molecular analysis (Figs. 1, 2).

The remaining three genera, *Thlaspeocarpa*, *Silicularia*, and *Schlechteria*, form a group characterized by lacking the septum and by having indehiscent fruits on recurved pedicels, but the features used in the separation of these three taxa (i.e., staminal appendages, habit) are also found in *Heliophila* and *Cycloptychis*. Therefore, it is not surprising to find *Thlaspeocarpa* in clade C as a relative to some *Heliophila* species (e.g., *H. crithmifolia*, *H. seselifolia*), all of which are annual herbs with appendaged staminal filaments.

Schlechteria and *Silicularia* are closely related, and they form a subclade in clade B, closest to *H. ephemera*, *H. nubigena*, and *H. tricuspidata*. Except for *H. ephemera*, these taxa are all perennial subshrubs. Bean (1990) stated that *H. ephemera* differs from the rest of *Heliophila* by having inflated fruits, spongy-walled seeds, coarsely tuberculate leaves, and intercalary racemes. Upon a critical study of the type material of *H. ephemera*, we conclude that the inflorescence is a typical rather than intercalary raceme. Interestingly, some *Heliophila* species (e.g., *H. cedarbergensis*, *H. esterhuyseniae*, *H. scoparia*, *H. dregeana*, *H. tulbaghensis*), *Schlechteria*, and *H. ephemera* share in clade B the apiculate anthers and one or a few seeds per locule. However, except for the presence of basal appendages on the filaments and their absence on petals, species of lineage B are not characterized by a consistent character pattern (Fig. 1).

The five smaller genera (*Brachycarpaea*, *Cycloptychis*, *Schlechteria*, *Silicularia*, *Thlaspeocarpa*) nested in *Heliophila* s. str. are distinguishable by a combination of (rather than unique) morphological characters all found within the *Heliophila* clades B and C. In our opinion, the maintenance of these genera as distinct from *Heliophila* would mean that a paraphyletic *Heliophila* has to be recognized, a position we do not support. Therefore, these five genera have been reduced to synonymy of *Heliophila* (Al-Shehbaz & Mummenhoff, 2005).

Infrageneric classification and taxonomic status of component genera of tribe Heliophileae

Previous infrageneric classification schemes in *Heliophila* (Candolle, 1821; Sonder, 1846) relied heavily on fruit morphology. However, the most recent taxonomic treatment of the genus (Marais, 1970) did not recognize any sections. Recent molecular studies in the Brassicaceae clearly demonstrated convergence in almost every fruit character (Koch et al., 2003, and references therein), and the current study further supports that conclusion. Although Sonder (1846) did not have knowledge of all species included in this study, none of his sections represents a monophyletic group. Instead, species of his sections are uniformly distributed among all three main clades in the molecular tree (Figs. 1, 2). Thus, the fruit types used by Sonder to distinguish sections are not synapomorphies and evidently evolved independently in the different lineages of *Heliophila*.

The molecular splitting of *Heliophila*, together with the nested *Brachycarpaea*, *Cycloptychis*, *Schlechteria*, *Silicularia*, and *Thlaspeocarpa*, in three clades (A–C in Figs. 1, 2) correlates quite well with the distribution of morphological characters. These character combinations (see below) were not adequately accounted for in previous taxonomic treatments.

Species of clade A are typically annual herbs (rarely perennials, as in *Heliophila subulata* and *H. linearis*) with "exstipulate," entire leaves (*H. arenaria*, *H. digitata*, and *H. macowaniana* have pinnately lobed leaves), basally appendaged staminal filaments and frequently also petals (*H. subulata* has unappendaged filaments and petals), and smooth, often wingless seeds (*H. linearis* and *H. cornuta* have winged seeds).

Optimization of different habits (Figs. 1, 6) shows that species of clade B are shrubs/subshrubs (only *Heliophila ephemera* is herbaceous) with exclusively unappendaged staminal filaments and petals, simple leaves, wingless seeds (only *H. scoparia* with winged seeds), and apiculate anthers (*H. macra* and *H. elongata* with unapiculate anthers). Within clade B, a terminal, well-supported (78% jackknife value) subclade, which includes *H. cedarbergensis*, *H. esterhuysensiae*, *H. scoparia*, *H. dregeana*, and *H. tulbaghensis*, is readily distinguished from the entire Heliophileae by having intercalary inflorescences (rather than typical racemes) and a generally papillate (vs. smooth) seed coat.

Species of clade C exhibit a mosaic of the character states also occurring in clades A and B. All species of this clade have smooth seeds, racemes, and latiseptate fruits (*Heliophila cornellsbergia* has inflated fruits). The vast majority of members of this clade are annuals, but *H. carnosa* and *H. suavissima* are perennial subshrubs that produce annual shoots from a woody crown. Optimization on the cladogram indicates that these morphological deviations represent secondary reversals. Furthermore, the development of the seed wing seems to be a primitive feature in the clade, and wingless seeds evolved independently in a subclade including *H. collina*, *H. pubescens*, and *H. pectinata*, as well as in *H. arenosa*. The clade also shows a mosaic pattern in the presence of small "bracts" at the base of pedicels, minute "stipules" at the leaf base, as well as in the development of basal appendages on the petals and stamens.

The small appendages at the pedicel bases in the Heliophileae were interpreted as "stipules" or otherwise completely reduced "bracts" (Marais, 1970; Appel & Al-Shehbaz, 2003), but functionally they probably represent extrafloral nectaries. Further studies of Bean (1990) revealed their presence in *Chamira* and all other genera of the Heliophileae except *Cycloptychis*. Such "bracts" are typically found in nearly all species of clades B and C, and their absence in a few species of these clades most likely represents parallel losses. It further appears that the absence of "bracts" is diagnostic for all species of clade A except *Heliophila subulata*.

The recognition of monotypic and ditypic genera in the Heliophileae mirrors several other cases in the Brassicaceae where differences in fruit characters often are overemphasized at the expense of taxonomically more useful other characters. Koch et al. (2003) listed several such examples, including *Twisselmannia* Al-Shehbaz versus *Tropidocarpum* Hook., *Thlaspi* L. versus *Alliaria* Scop., and *Lepidium* versus *Coronopus* Zinn. Ideally, a critical evaluation of the taxonomic status of the *Heliophila* s.l. clades (e.g., generic vs. subgeneric level) should await more sequence data from other markers and more extensive sampling of the ingroups and outgroups.

Morphological character evolution

Despite the incompleteness of our study, one can safely make some generalizations regarding the evolution of certain features (Fig. 1). For example, intercalary inflorescences and papillate seeds apparently evolved only once within a terminal subclade of clade B that includes *H. cedarbergensis*, *H. esterhuyseniae*, *H. scoparia*, *H. dregeana*, and *H. tulbaghensis*. On the other hand, apiculate anthers also probably evolved once at the base of clade B, with reversals in both *H. macra* and *H. elongata*. By contrast, the evolution of indehiscent, one- or two-seeded fruits occurred independently in *Thlaspeocarpa* of clade C and at least twice in clade B: in the subclade containing *Brachycarpaea* and *Cycloptychis* as well as that including *Schlechteria*, *Silicularia*, and *H. ephemera*. Wingless seeds appear to be basal in each of clades A and B, and it is likely that winged seeds might be basal in clade C. It seems that the shift from one seed type to another occurred several times within *Heliophila* s.l. Finally, taxa with entire leaves appear to be basal in the entire genus *Heliophila* s.l., and pectinate or pinnately lobed leaves with filiform or narrowly linear segments evolved secondarily in clades A and C (Fig. 1).

Fruit diversity within Heliophileae has no match anywhere in the Brassicaceae. For example, fruit length ranges from long siliques to minute silicles, fruit compression varies from latiseptate, terete, to angustiseptate, and upon maturity, the fruits may

be dehiscent, indehiscent, or even schizocarpic (Marais, 1970; Appel & Al-Shehbaz, 1997, 2003). The result of mapping fruit morphologies onto the phylogenetic trees (Fig. 2) suggests that fruit characters are quite variable even within each of the three main clades of *Heliophila*. On the basis of the present molecular studies, one can trace fruit evolution from latiseptate and unconstricted (smooth) to moniliform siliques (e.g., *H. dregeana* and *H. tulbaghensis* in clade B); from latiseptate silicles to schizocarpic (*Cycloptychis*) and angustiseptate-didymous (*Brachycarpaea*); and from latiseptate and dehiscent siliques to indehiscent silicles (*Thlaspeocarpa*). Furthermore, it appears that schizocarpic fruits in the Heliophileae evolved once in the subclade including *Brachycarpaea* and *Cycloptychis*. The occurrence in each of the three *Heliophila* subclades of the same fruit types demonstrates convergent/parallel evolution (Fig. 2). For example, moniliform fruits evolved independently in each of clades A, B, and C, though they appear to have evolved once within clade B in a well-supported (100% bootstrap) subclade that includes *H. dregeana* and *H. tulbaghensis* (Fig. 1).

It is important to note that fruit dehiscence and relative length, both of which are major diagnostic characters for generic delimitation in the traditional systems of Hayek (1911) and Schulz (1936), are controlled in *Arabidopsis thaliana* by the single MADS-box genes *SHATTERPROOF* and *FRUITFUL* (Liljegren et al., 2000; Ferrandiz et al., 2000). Such a relatively simple control of fruit morphology (dehiscence/indehiscence, relative length) would easily explain the rapid and independent evolution of multiple fruit types within various genera of the Brassicaceae, including *Heliophila*. One suspects that such simple inheritance controlling drastic morphological differences might hold true for the other characters addressed above.

We think it likely that the number of genes controlling the remarkable differences in fruit morphology are relatively few, thus allowing rapid evolutionary changes independent of other aspects of morphology. The high degree of sequence similarity between several species of *Heliophila* and members of the five smaller genera (*Brachycarpaea*, *Cycloptychis*, *Schlechteria*, *Silicularia*, and *Thlaspeocarpa*) strongly emphasizes the apparent rapidity with which drastic changes in fruit morphology can sometimes occur in the family, thus leading to classifications or generic delimitations that obscure rather than clarify evolutionary relationships. As suggested by Koch et al. (2003), future molecular studies would most likely reveal that the vast majority of monotypic and oligotypic genera of the Brassicaceae should be reduced to synonymy of larger genera, and our present study strongly supports that hypothesis.

In conclusion, we have demonstrated that the heavy reliance on fruit characters alone may well lead to erroneous taxonomic results and that such characters should be critically evaluated in light of the molecular and other morphological data (Koch et al., 2003, and references therein). A critical evaluation of morphology in *Heliophila* and allies reveals that the individual characters vary in their value for systematic classification (see above). As demonstrated by Bailey et al. (2002) for the Halimolobine Brassicaceae, it appears that a combination of morphological characters is potentially useful in classification, and as demonstrated above, we believe that this also holds within Heliophileae.

Cytology

Hardly anything is known about the chromosome numbers in the Heliophileae. The four species studied, all with $2n = 20$, are *Heliophila africana* (as *H. pilosa*), *H. amplexicaulis*, *H. crithmifolia*, and *H. linearis* (Jaretzky, 1932; Manton, 1932). However, these counts were based on material grown in botanical gardens, and no vouchers are available to verify the identity of the taxa involved.

DATING THE RADIATION

Using different approaches to calibrate our trees (i.e., the 22 mya for the Brassica/Cleome clade from Wikström et al. (2001), or a range of published angiosperm rDNA ITS substitution rates (see Results)), we arrive at age estimations of 2–5 mya for the proliferation of the Heliophileae (see Table 3). The NPRS smoothing algorithm consistently estimates older ages, but not more than around 5 mya. Given that the dates from Wikström et al. (2001) may be far too young, our age estimation for the Heliophileae proliferation could be up to 10 mya maximally. On the other hand, the observation that our published rDNA ITS substitution rate-based estimate is remarkably similar to the "forced clock"-derived estimation, combined with the notion that NPRS tends to overestimate ages, suggests a more recent age of 2–5 mya. If accurate, the amazing range of morphological variation observed in Cape *Heliophila* species would thus have been generated within a Pliocene–Pleistocene time frame. Such an estimate suggests a considerably faster rate compared with radiations in other Cape genera, such as *Pelargonium* L'Hér. (Geraniaceae) and *Phylica* L. (Rhamnaceae), for both of which Miocene age was suggested (Bakker et al., 2005; Richardson et

al., 2001), and Restionaceae, for which an Oligocene age was proposed (Linder & Hardy, 2004).

Our estimate would also constitute the most recent Cape radiation reported so far, which is much earlier than the 8–32 mya range given by Linder (2003) and Linder and Hardy (2004) for the Cape Floral Region crown clade proliferations. Most of the Cape-clade radiation dates are based on NPRS-derived ultrametric trees, and several rely on the Wikström et al. (2001) dates for calibration. At the moment there does not appear to be an indication of simultaneous radiation in these lineages. Clearly, a meta-analysis needs to be conducted in which calibration and ultrametricity are arrived at in a concerted approach.

ECO-GEOGRAPHICAL EVOLUTION IN *HELIOPHILA*

The three major clades of *Heliophila* s.l. can be largely characterized in terms of distribution patterns and habit (Figs. 4, 6). Distribution patterns also reflect rainfall gradients, vegetation type, and bedrock types. Our crude data make it impossible to achieve a finer resolution of the eco-geographical patterns.

Clade B, which exclusively includes shrubs or subshrubs (except for the herbaceous *Heliophila ephemera*), is almost completely restricted to the CFR (Cedarberg-Nieuwoudtville, Swartruggens, central Cape mountains, southern Cape), with an ancestral distribution optimized as restricted to the CFR (Fig. 4). Its species mostly grow on soils derived from Table Mountain sandstone (Fig. 8), very often among boulders or on rock ledges (Fig. 5), and in fynbos and renosterveld (Fig. 7). Fire is a regular occurrence in fynbos vegetation, with a frequency of 5–50 years (van Wilgen, 1987), and several species show adaptations to survive after fire by resprouting (Schutte et al., 1995). The associations with rock might also indicate habitats somewhat protected from fire. The distribution pattern suggests a rainfall range of 300–2000 mm, with dry summers. The optimizations indicate an ancestral occurrence on sandstone, and in fynbos, with several expansions on shale soils and into renosterveld vegetation. Furthermore, clade B can be divided into an eastern subclade (clade B1 in Fig. 4), the species of which grow in areas that receive more summer rain and contain several Eastern Cape species. Clade B2 in Figure 4, which is centered more to the north, has no representatives in the summer-wet Eastern Cape, but its species grow in the arid Swartruggens that receive no rain in the summer and very little in the winter. The only annual species, *H. ephemera*, is not ecologically different from the other members of clade B.

Clade A, which consists largely of annuals (Fig. 6), is also centered in the CFR with an ancestral distribution optimized as restricted to the CFR (Fig. 4). It has a wider range of outliers than clade B (three species reach the Kamiesberg and two the Roggeveld mountains); these are interpreted as dispersal from the CFR. Although most species show the typical CFR syndrome (i.e., occurring in fynbos heathy pyrophytic vegetation and growing on sandstone-derived soils, Figs. 7, 8), the ancestral situation is uncertain, and the optimizations indicate that the basal nodes are polymorphic. The two coastal species of *Heliophila* belong to this clade, and they occur on limestone or coastal dunes, mostly on alkaline sand, and in non-pyrophytic strandveld. These represent two invasions of this habitat by *H. subulata* and *H. linearis*.

Clade C, also including mostly annuals (Fig. 6), is centered on the Richtersveld in Karooid vegetation, with an ancestral distribution optimized to be either the Richtersveld or the Richtersveld and the Roggeveld. Its species grow on sandy, loamy, or clayey soils derived from shale or granite (Figs. 5, 8). These areas are generally arid, have hot dry summers and short winters, and receive less than 400 mm of annual rainfall. They are generally rich in annuals, possibly due to a combination of very harsh summers and relatively rich soils (Pienaar & Nicholas, 1988) that allow rapid growth in the short, winter-spring favorable season.

The three Drakensberg species (*Heliophila carnosa*, *H. rigidiuscula*, and *H. suavissima*) are nested in this group C, and placed in two subclades. These species indicate two range extensions from the Richtersveld to the east (Fig. 4), as well as a change from annual to perennial habit (Fig. 6). In addition, they indicate a shift from sparse winter-rainfall (less than 300 mm annually and without frost), to wet summer-rainfall areas with frequent winter snow. It is a remarkable ecological range extension also matched by *Pentaschistis airoides* Stapf and several other grasses (Linder & Ellis, 1990). Possibly the harsh alpine environment of the Drakensberg has similarities to the harsh semidesert environment of the Namaqualand escarpment. The other two Drakensberg *Heliophila* species, *H. alpina* and *H. formosa*, were not included in this study, and it is unclear whether they also group with the above three species. The only other species from KwaZulu-Natal included in this analysis is the coastal *H. elongata*, a species that also grows in the Eastern Cape and that groups basally into Clade B1 in Figure 4.

Four species, *Heliophila eximia*, *H. deserticola*, *H. trifurca*, and *H. crithmifolia*, show an expansion into the arid Namib desert in which none is endemic (Fig. 4). Of these, *H. eximia* is a perennial, a habit that goes against the general trend of the annual *Heliophila* species found in seasonally arid areas. However, this species is found only in southern Namibia, and it might be considered as a member of the Richtersveld biogeographical region.

The Roggeveld is biogeographically interesting because it forms the border between the CFR and the Gordonia region. There are no species of clade B in this region, while clade A is represented by its most widespread species, *Heliophila cornuta*, as well as *H. acuminata*, which is also found in the adjacent Cedarberg. Clade C is represented by 8 of its 17 species in the region, which can be regarded as the center for clade C.

Evidently, the perennial species are associated with wetter or at least summer-wet areas, while the annuals occupy the more arid western half of the subcontinent. If the annual habit is assumed to be primitive in *Heliophila* s.l., then the perennial habit (Fig. 6) evolved independently at least seven times and was lost once (*H. ephemera*). The habit seems to be tightly correlated with macro-ecology and phylogeny, but it is unclear whether or not a change of habit allowed the species to be established in the Drakensberg region.

ADAPTIVE SHIFTS/FACTORS EXPLAINING THE RADIATION IN *HELIOPHILA*

Goldblatt and Manning (2000) and Linder (2003) suggested that the remarkable species richness in the CFR might be the consequence of diverse limitations to gene flow (e.g., dissected landscapes, pollinator specialization, long flowering times allowing much phenological specialization) and a complex environment providing a diversity of selective forces (e.g., geographical climatic variation, altitudinal variation, different soil types, regular fires). Due to the lack of experimental and observational studies on the adaptive significance of various structures, morphology will be used to infer the various functions of these structures. This approach should result in a predictive framework on which experimental studies can be based.

In addition to the diversity in flower color and size (see the introductory paragraphs), the differences in inflorescence and flower structure obviously are linked to different pollinators or pollination strategies (Johnson, 1996; Linder, 2003, and references therein; Perret et al., 2003; Bakker et al., 2005). The inflorescence in *Heliophila* species is typically a raceme, but it is intercalary in five species of clade B (Fig. 1), which means that the terminal flower is overtopped by new leafy growth of the central axis (Marais, 1970; Bean, 1990). In these intercalary inflorescences the growth recommences after a first flush of flowers, thus potentially lengthening flowering time and allowing specialization. The majority of Brassicaceae have flowers with visible nectaries and easily accessible nectar for the visiting insects, such as short-proboscid flies, wasps, or beetles (Knuth, 1898; Schultze-Motel, 1986). Species of many genera have tubular (e.g., *Matthiola* R. Br.) or internally appendaged flowers (*Heliophila*) in which the nectar is hidden, and their flowers are pollinated by long-proboscid insects such as bees, bumblebees, moths, and butterflies (Knuth, 1898; Kugler, 1955; Schultze-Motel, 1986; Procter et al., 1996). Both appendaged and unappendaged flowers are found in *Heliophila*, and species of clades A and C are typically characterized by basal appendages on the petals and staminal filaments (Fig. 1).

Schulz (1931) suggested that the floral basal appendages in *Heliophila* are associated with the nectaries and often hide them. We suggest that the basal appendages of petals and filaments, which allow insects with longer rather than shorter probosces to access nectar, play a selective role that may promote interspecific reproductive isolation and therefore may increase speciation rates and diversification. Unfortunately, hardly anything is known about the floral biology of *Heliophila* species, and extensive field studies would most likely provide pollination data valuable to understanding the adaptive radiation of the genus in South Africa.

The leaves and pedicels of many species of clades B and C are basally subtended by small appendages interpreted as "stipules" or "bracts" (Marais, 1970; Appel & Al-Shehbaz, 2003) but functionally may represent extrafloral nectaries. If nectaries, they might attract insects and prevent pollination between neighboring flowers of the same inflorescence. Ants are poor cross-pollinators and are attracted to extrafloral nectaries (Chauhan, 1979), but it is unknown if they play any such role in *Heliophila*. In some species of clade A (e.g., *H. linearis*, *H. namaquana*, *H. africana*), Schulz (1931) described swollen clavate styles in the ripe fruits. Although the adaptive significance of these structures is unknown, Schulz (1931) suggested that they might represent a food offer to herbivores to prevent seed damage when snipped off.

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Appendix 1. Collection data and GeneBank accession numbers of South African endemic Brassicaceae species studied.

Species[1]	Provenance[2] / Herbarium-source[3] / Collector[4]	Gen Bank accession number	
		ITS I	ITS II
Heliophila acuminata (Eckl. & Zeyh.) Steud.	South Africa, SW, Malmesbury district, Klein Swartfontein, near Moorreesburg, 33°08′S, 18°39′E / PRE / *Acocks 24401*	AJ863603	AJ864807
H. africana 1 (L.) Marais	South Africa, SW, Cape Town, 33°52′S, 18°31′E / NBG / *Steiner 1975*	AJ863602	AJ864808
H. africana 2 (L.) Marais	South Africa, Cape Peninsula, Olifantbos Bay / OSBU / *Neuffer 9402*	AJ863601	AJ864809
H. amplexicaulis L.f.	South Africa, NW, SW, KM / cultivated, Botanic Garden Paris, France	AJ863611	AJ864810
H. arenaria Sond.	South Africa, NW, Clanwilliam Distr., between Nardouws Pass and Brakvlei, 33°10′S, 18°55′E / PRE / *Marais 1436*	AJ863600	AJ864811
H. carnosa (Thunb.) Steud.	South Africa, N, Ceres Div., Baviaansberg, 33°08′S, 19°37′E / BOL / *Esterhuysen 29796*	AJ863599	AJ864805
H. cedarbergensis Marais	South Africa, NW, Clanwilliam Distr., Langeberg, Central Cedarberg Mountains / BOL / *Esterhuysen 35055*	AJ863607	AJ864812
H. collina O. E. Schulz	South Africa, NW, Calvinia, Nieuwoudtville Reserve, 31°22′S, 19°07′E / NBG / *Perry & Snijman 2199*	AJ863598	AJ864813
H. cornellsbergia B. J. Pienaar & Nicholas	South Africa, NW, Richtersveld, Cornellsberg in Stinkfontein Mts. Southern slopes to a neck S of top / PRE / *Oliver, Tölken & Venter 715*	AJ863576	AJ864803
H. cornuta Sond.	South Africa, Ceres Div., Zwartruggens, Groenfontein, near Stompiesfontein, 33°05′S, 19°19′E / BOL / *Bean & Trinder-Smith 2686*	AJ863597	AJ864804
H. coronopifolia 1 L.	South Africa, SW, Caledon, foot of Hoys Koppie, Hermanus, 34°25′S, 19°14′E / MO / *Williams 982*	AJ863596	AJ864814
H. coronopifolia 2 L.	Cultivated / Botanical Garden Halle, Germany	AJ863592	AJ864817
H. coronopifolia 3 L.	Cultivated / Botanical Garden Aarhus, Denmark	AJ863588	AJ864824
H. crithmifolia 1 Willd.	South Africa, NW, in between Clanwilliam and Wuppertal, road side, 32°13′S, 19°10′E / OSBU / *Neuffer 9258*	AJ863577	AJ864799
H. crithmifolia 2 Willd.	South Africa, LB, KM, South Cape district, Oudtshoorn, next to turnoff to Blossoms, 33°33′S, 22°11′E / BOL / *Vlok 1048*	AJ863595	AJ864806
H. descurva Schltr.	South Africa, Cedarberg Mts., near Wuppertal, 32°16′S, 19°13′E / OSBU / *Neuffer 9253*	AJ863575	AJ864815
H. deserticola Schltr.	Namibia, Oranjemund, 5 km N of Oranje near Sendelingsdrif, 28°09′S, 16°53′E / MO / *Giess & Müller 14375*	AJ863594	AJ864798
H. digitata L.f.	South Africa, Clanwilliam, Farm Suurfontein / NBG / *Whitehead s.n.*	AJ863593	AJ864816
H. dregeana Sond.	South Africa, Cold Bokkeveld, Elands Kloof at Twee Riviren / MO / *Goldblatt 2578*	AJ863606	AJ864818
H. elongata (Thunb.) DC.	South Africa, forests near Knysna, 34°01′S, 23°03′E / MO / *Lavranos 6203*	AJ628255	AJ628256
H. ephemera P. A. Bean	South Africa, Oudtshoorn Prov., Swartberg, northern slopes, 4 km E of Blouberg on Botha's track / MO / *Viviers, Vlok & Bean 1551*	AJ628257	AJ628258
H. esterhuyseniae Marais	South Africa, Caledon Prov., Franschhoek Mountains, Roesbos Peak, 33°54′S, 19°08′E / BOL / *Esterhuysen 29422*	AJ628259	AJ628260
H. eximia Marais	South Africa, N, Richtersveld, Kodaspiek, main ridge SE of Beacon and up to summit, 28°32′S, 17°05′E / PRE / *Oliver, Tölken & Venter 390*	AJ863591	AJ864819
H. gariepina Schltr.	South Africa, N, Richtersveld, Kodaspiek, main ridge SE of Beacon and up to summit, 28°32′S, 17°05′E / PRE / *Oliver, Tölken & Venter 476*	AJ863590	AJ864820

Appendix 1. Continued.

Species[1]	Provenance[2] / Herbarium-source[3] / Collector[4]	Gen Bank accession number	
		ITS I	ITS II
H. glauca Burch. ex DC.	South Africa, Ladismith Div., Anysberg, N slopes, 33°30′S, 20°46′E / MO / *Esterhuysen 32859*	AJ863610	AJ864821
H. linearis (Thunb.) DC.	South Africa, Mossel Bay, between Outeniquastrand and Tergniet, 34°03′S, 22°12′E / BOL / *Vlok 1949*	AJ863589	AJ864822
H. macowaniana Schltr.	South Africa, road from Clanwilliam and Cape Town, 20.5 km from Clanwilliam, road side, 32°21′S, 18°56′E / PRE / *Marais 1447*	AJ863587	AJ864825
H. macra Schltr.	South Africa, Caledon Div., Hermanus, Fernkloof Nature Reserve, above Northcliff, 34°25′S, 19°14′E / MO / *Robertson 134*	AJ863609	AJ864826
H. macrosperma Burch. ex DC.	South Africa, Albany, Fish River Pass, 33°17′S, 26°47′E / MO / *Bayliss 2257*	AJ863608	AJ864827
H. minima (Stephens) Marais	South Africa, Richmond Distr., 31 km NW of Merriman Station, 30°59′S, 23°33′E / PRE / *Acocks 24430*	AJ863586	AJ864828
H. namaquana Bolus	South Africa, Clanwilliam Dist., Pienaarsvlakte between Krom River and Matjiesriver / BOL / *Bean 1345*	AJ863585	AJ864802
H. nubigena Schltr.	South Africa, Worcester Dist., Keeromsberg / BOL / *Esterhuysen 33671*	AJ863613	AJ864829
H. pectinata Burch. ex DC.	South Africa, Ceres-Clanwilliam road via Groot, turnoff to farm Kleinveld, S of Blinkberg Pass / PRE / *Marais 1416*	AJ863584	AJ864830
H. pubescens Burch. ex DC.	South Africa, Calvinia, Kleinfontein, Agterkop, Pk. Middelpos, 32°01′S, 20°04′E / PRE / *Hanekom 2138*	AJ863583	AJ864831
H. pusilla L.f.	South Africa, Caledon, Hermanus, Die Duine, 34°25′S, 19°14′E / PRE / *Williams 1264*	AJ863582	AJ864832
H. rigidiuscula Sond.	South Africa, Mkambati, road to Lupatana, 31°19′S, 29°57′E / MO / *Hutchings 727*	AJ863572	AJ864797
H. scoparia Burch ex DC.	South Africa, Worcester Dist., Hex Rivier Mts., Audensberg, 33°28′S, 19°34′E / BOL / *Esterhuysen 28193*	AJ863605	AJ864833
H. seselifolia Burch. ex DC.	South Africa, Williston Dist., Snyderspoort through the Basterberge, 31°20′S, 20°55′E / STE / *Thompson 3161*	AJ863581	AJ864801
H. suavissima Burch. ex DC.	South Africa, Orange Free State, Glen Landboukollege / PRE / *PC & L. Zietsman s.n.*	AJ863574	AJ864834
H. subulata Burch. ex DC.	South Africa, Riversdale, Stillbaai, ridge below reservoir, 34°22′S, 21°26′E / STE / *Bohnen 5223*	AJ863580	AJ864835
H. tricuspidata Schltr.	South Africa, Caledon Dist., Jonas Kop, Langeberg, NW of Genadendal, 34°01′S, 19°36′E / BOL / *Esterhuysen 32705*	AJ863612	AJ864836
H. trifurca Burch. ex DC.	South Africa, Namaqualand, road from Garies via eastern mountains to Springbok, 30°07′S 17°59′E / OSBU / *Neuffer 9280*	AJ863604	AJ864800
H. tulbaghensis Schinz	South Africa, Paarl Dist., path from Fransch Hoek Pass towards Paardekoop, near head of valley, 33°54′S, 19°09′E / BOL / *Esterhuysen 35692*	AJ863579	AJ864837
H. variabilis Burch. ex DC.	South Africa, Richtersveld, top of Hellskloof, road going to Springbokvlakte / STE / *Nicholas 2511*	AJ863578	AJ864838
Brachycarpaea juncea (Bergius) Marais	South Africa, Clanwilliam Dist., Berg Road / NBG / *Barker 10426*	AJ862707	AJ862708
Chamira circaeoides (L.f.) Zahlbr.	South Africa, Malmesbury Dist., Bokbaai, 33°34′S, 18°21′E / BOL / *Bean & Viviers 1901*	AJ862719	AJ862720
Cycloptychis marlothii O. E. Schulz	South Africa, Ceres Dist., Zwartruggens, Groenfontein, near Stompiesfontein in rugged refugium in TMS ridge, 32°59′S, 19°01′E / BOL / *Bean & Trinder-Smith 2687*	AJ862709	AJ862710
Cycloptychis virgata (Thunb.) E. Mey. ex Sond.	South Africa, Piketberg Dist., Piketberg Mts. near Piketberg, 32°53′S, 18°43′E / NBG / *Barker 10341*	AJ862711	AJ862712

Appendix 1. Continued.

Species[1]	Provenance[2] / Herbarium-source[3] / Collector[4]	Gen Bank accession number	
		ITS I	ITS II
Schlechteria capensis Bolus	South Africa, Clanwilliam Dist., Wolfberg, N Cedarberg, 32°28′S, 19°08′E / BOL / *Esterhuysen 29984*	AJ862715	AJ862716
Silicularia polygaloides (Schltr.) Marais	South Africa, Ceres Dist. / BOL / *Leighton 2288*	AJ862713	AJ862714
Thlaspeocarpa capensis (Sond.) C. A. Sm.	South Africa, Sutherland, Voelfontein, valley S of farm house on road to mountain, 32°23′S, 20°39′E / MO / *Goldblatt 6319*	AJ862717	AJ862718
Alliaria petiolata (M. Bieb.) Cavara & Grande	Campus area University of Osnabrück, Germany, 52°16′N, 7°59′E	AJ862703	AJ862704
Aethionema saxatile (L.) R. Br.	Cultivated, Botanical Garden of the University of Osnabrück, Germany, 86 30 096 14	AJ862697	AJ862698
Rorippa amphibia (L.) Besser	Germany, Cologne / *M. Koch s.n.*	AF078025	AF078524
Cardamine matthioli Moretti	Slovakian Republic, Slovenské Rudohorie Mountains, near Brezno, 48°44′N, 19°51′E / OSBU / *Franzke 11 / 6*	AF077985	AF077986
Cleome spinosa Jacq.	Cultivated, Botanical Garden of the University of Osnabrück, Germany	AY254535	AY254535

[1] Nomenclature follows Jordaan (1993).

[2] Phytogeographic centers are given by abbreviation in capital letters (Goldblatt & Manning, 2000).

[3] BOL: Bolus Herbarium, University of Cape Town, South Africa; MO: Missouri Botanical Garden, Saint Louis, Missouri, U.S.A.; OSBU: Herbarium University of Osnabrück, Germany; PRE: National Botanical Institute, Pretoria, South Africa; STE: National Botanical Institute, Stellenbosch, South Africa; NBG: Compton Herbarium, National Botanical Institute, Claremont, South Africa.

[4] Collector with collection number.

CONGRUENCE OF A PHYLOGENY OF CORDIACEAE (BORAGINALES) INFERRED FROM ITS1 SEQUENCE DATA WITH MORPHOLOGY, ECOLOGY, AND BIOGEOGRAPHY[1]

Marc Gottschling,[2,3] *James S. Miller,*[2] *Maximilian Weigend,*[3] *and Hartmut H. Hilger*[3]

Abstract

The phylogenetic relationships of Cordiaceae were investigated using ITS1 sequences from 50 ingroup taxa and three outgroup taxa. Molecular analyses suggest that *Coldenia procumbens*, traditionally placed in Ehretiaceae, is more closely allied to Cordiaceae and is sister to their core representatives. Cordiaceae segregate into four major monophyletic assemblages, more or less corresponding to established taxonomic units as previously inferred from morphology, ecology, and biogeography. (1) Varronia (currently recognized as *Cordia* sect. *Varronia*) is a well-differentiated taxon and has a sister-group relationship to the other three clades (*Cordia* s. str.). The (2) Collococcus clade comprises the New World species of *Cordia* sect. *Myxa* (excluding *Cordia dentata* and *Cordia lutea*), all of *Cordia* sect. *Superbiflorae*, and *Cordia varronifolia* (from *Cordia* sect. *Rhabdocalyx*). The (3) Myxa clade includes all of the Old World species of *Cordia* sect. *Myxa* and the New World species *Cordia dentata* and *Cordia lutea*. The (4) Sebestena clade includes *Cordia* sects. *Cordia* and *Gerascanthus*, three species of *Cordia* sect. *Rhabdocalyx*, and *Auxemma*, *Patagonula*, and *Saccellium*. Pollen morphology and wood anatomy lend additional support for the close relationship of *Auxemma*, *Patagonula*, and *Saccellium* with *Cordia sebestena* and its allies. Thus, *Auxemma*, *Patagonula*, and *Saccellium* are no longer tenable as separate taxa and should be reduced under *Cordia*. A set of ancestral characters (including apomorphies and plesiomorphies) is reconstructed for Cordiaceae based on the phylogenetic hypotheses as inferred from the congruence between morphological and ITS1 data.

Key words: *Auxemma*, Boraginales, *Cordia*, ITS1 sequence data, molecular systematics, *Patagonula*, phylogeny, *Saccellium*, secondary structure, *Varronia*.

Boraginaceae have traditionally been subdivided into the four taxonomic units Boraginoideae, Heliotropioideae, Cordioideae, and Ehretioideae (Candolle, 1845; Gürke, 1893). Recent molecular and morphological studies confirm the monophyly of each of the four subordinate taxa, but suggest that Boraginaceae are only monophyletic when Hydrophyllaceae and parasitic Lennoaceae are also included (Böhle & Hilger, 1997; Gottschling et al., 2001; Diane et al., 2002; Diane, 2003; Gottschling, 2003; Hilger & Diane, 2004). Therefore, we follow the systematic concept of Thorne (1983), who recognized the close relationship of the subordinate taxa of Boraginaceae, sensu Gürke (1893), with Hydrophyllaceae and Lennoaceae, and use a classification of Boraginales with the subordinate taxa Boraginaceae s. str., Hydrophyllaceae s. str. (i.e., excluding *Hydrolea* L.; Ferguson, 1999), Heliotropiaceae, Ehretiaceae (including *Lennoa* Lex. and *Pholisma* Nutt. ex Hook.), and Cordiaceae. Heliotropiaceae, Ehretiaceae, and Cordiaceae are parts of one monophyletic group based both on molecular (Gottschling et al., 2001) and on morphological data (multilayered endocarp; Diane et al., 2002) and constitute the Primarily Woody Boraginales (sensu Gottschling, 2003).

In its traditional circumscription, *Cordia* L. comprises about 350 species that are pantropical in

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[2] Missouri Botanical Garden, P.O. Box 299, St. Louis, Missouri 63166-0299, U.S.A. caix@zedat.fu-berlin.de (M. Gottschling), james.miller@mobot.org.

[3] Freie Universität Berlin, Institut für Biologie–Systematische Botanik und Pflanzengeographie–Altensteinstraße 6, D–141 95 Berlin, Germany. weigend@zedat.fu-berlin.de, hahilger@zedat.fu-berlin.de.

distribution, with centers of diversity in the tropical Americas and to a lesser extent in Africa (Taroda & Gibbs, 1986; Gaviria, 1987; Verdcourt, 1991; Miller, 2001). The group is well represented in countries such as Mexico, Brazil, and Peru, where species of *Cordia* are most abundant in seasonally dry areas and are important elements of various plant communities such as tropical deciduous forests and shrub forest (of, e.g., the Andean matorral in inner-Andean valleys and on the western slope of the Andes). Furthermore, *Cordia* is also found in permanently wet habitats such as cloud forest and lowland rain forest. The plants are usually erect shrubs or trees, and scandent shrubs are found in *Cordia* sects. *Varronia* (P. Br.) G. Don (in cloud and montane rain forests from Peru northward through Mexico) and *Myxa* (Endl.) DC. (in East African savannas).

The other taxa traditionally included in Cordiaceae are *Auxemma* Miers (Brazil, two species) and *Patagonula* L. (Brazil, Paraguay, Bolivia, Argentina, two species). They are readily distinguished from *Cordia* on the basis of calyx characters: The sepals of *Patagonula* develop into long, rotor-shaped wings in the mature fruit, and *Auxemma* has an inflated calyx completely enclosing the drupe. Traditionally, *Saccellium* Humb. & Bonpl. (Bolivia, Brazil, Peru, Argentina, three species) has been placed in Ehretiaceae, but palynology (Nowicke & Miller, 1990) and fruit morphology as well as molecular data (Böhle & Hilger, 1997; Gottschling et al., 2001) demonstrate that *Saccellium* belongs to Cordiaceae. The monophyly of Cordiaceae in this circumscription is well supported both by molecular data (Gottschling et al., 2001) and by morphological apomorphies such as the presence of an undivided endocarp, four stigmatic lobes, and plicate cotyledons.

Classification of *Cordia* has been controversial because of the great morphological variation encompassed by its species. Most recent authors have treated *Cordia* in a traditional, wider sense (Miller, 1985; Taroda & Gibbs, 1986; Gaviria, 1987; Warfa, 1988; Verdcourt, 1991). Various authors have recognized from 5 to almost 20 subgenera, sections, and subsections for *Cordia*, and some attempts have been made to segregate *Cordia* into separate genera (Browne, 1756; Britton & Millspaugh, 1925; Friesen, 1933; Borhidi et al., 1988). Which species are to be included in these infrageneric categories is at least as confusing as the subdivisions themselves. Thus, *Cordia* sect. *Varronia* sensu Gürke (1893; based on Candolle, 1845) is a heterogeneous assemblage of distantly related species, while three of four subsections that Gürke (1893) placed under *Cordia* sect. *Myxa* really belong to *Cordia* sect. *Varronia*, as Johnston (1930) previously recognized. Similarly, various authors re-established or described new genera, which are paraphyletic or polyphyletic (e.g., *Varronia* P. Br. sensu Friesen, 1933; *Lithocardium* Kuntze of Kuntze, 1891). The taxonomical changes were at times far-reaching: About 170 new combinations and names were published for the generic segregate *Gerascanthus* P. Br., ". . . a rather varied group," with characters ". . . overlapping over the different taxonomic groups . . ." (Borhidi et al., 1988: 394–395), i.e., for an assemblage, which is truly unnatural.

The most comprehensive modern infrageneric classification of *Cordia* can be compiled from the scattered publications of Ivan M. Johnston. Initially, Johnston (1930) grouped the American species of *Cordia* into seven sections plus the Old World *Cordia* sect. *Myxa*, and later he reduced *Cordia* sects. *Physoclada* DC. (with the only species *C. nodosa* Lam.) and *Pilicordia* DC. under *Cordia* sect. *Myxa* (Johnston, 1951). This basic classification with five subordinate taxa was widely accepted by subsequent authors. Taroda and Gibbs (1986) recognized a group of South American species as distinct from *Cordia* sect. *Cordia* (= *Cordia* sect. *Eucordia* I. M. Johnst.) and segregated it as *Cordia* sect. *Superbiflorae* Taroda. Miller (2001) summarized their listing (with species numbers): *Cordia* sects. *Cordia* (approx. 20 New World species, 2 Old World species), *Gerascanthus* (P. Br.) G. Don (approx. 20 New World species), *Myxa* (more than 100 New World species, approx. 55 Old World species), *Rhabdocalyx* DC. (4 New World species), *Superbiflorae* (7 New World species), *Varronia* (approx. 100 New World species). This classification is here used as the taxonomic backdrop for the phylogenetic study of Cordiaceae.

The classification of *Cordia* is further complicated by the fact that its α-taxonomy is complex, and in the more species-rich groups identification is sometimes difficult. This is partly due to the extraordinarily high intraspecific variability (e.g., Gaviria, 1987; Miller, 1989), but also since new taxa have been airily described on the basis of poorly preserved herbarium specimens (e.g., Krause, 1906).

The present study aims at clarifying the phylogenetic relationships between the various groups in *Cordia* and *Auxemma*, *Patagonula*, and *Saccellium*, using sequence data from the First Internal Transcribed Spacer region (ITS1), the group I-intron $trnI_{(UAA)}$, and morphological features. Enigmatic species such as *C. bordasii*, *C. decandra*, and all representatives of the heterogeneous *Cordia* sect.

Rhabdocalyx were included to clarify their systematic placements. *Coldenia procumbens* has been traditionally assigned to Ehretiaceae (Gürke, 1893; Johnston, 1951; Verdcourt, 1991) as inferred from the (plesiomorphic) only once bifid style, but appears to be closely related to Cordiaceae based on molecular data from the *trn*L-intron (Hilger & Gottschling, unpublished). Thus, this species is also included in the analysis (although it lacks the characteristic apomorphies of the core Cordiaceae).

A secondary structure model of the ITS1 transcript has been proposed for Boraginales (Gottschling et al., 2001) that might be present in the majority of the Asteridae. This model consists of an open multibranch loop, with four pairing regions ('hairpins' or helices I to IV). Additional characters as inferred from the secondary structure such as length variation of helices are here used for the evaluation of the ITS1 sequences. Principally, secondary structure alignments are performed considering homologous regions within the molecule under investigation by mutual sequence comparison. The significance of the secondary structure for alignments and an instructive example of its application are extensively discussed in the review of Coleman (2003).

Materials and Methods

Fifty species of Cordiaceae were included in the present study (Table 1), covering largely the diversity of the taxon and including representatives from all subordinate taxonomic units that have been established so far. Representatives of Ehretiaceae and Heliotropiaceae were used for the user-specified outgroup comparison. DNA was obtained from specimens at the herbaria B, KUN, M, and MO and/or from silica-dried leaves from our own field trips (Mexico, Panama: Miller et al. in 1983, 1987, 1991; Cuba: Hilger in 1999, Gottschling in 1999; Peru: Weigend et al. in 2000, 2001).

DNA extraction, PCR, purification, and sequencing followed standard protocols, which are described in detail in Gottschling and Hilger (2001). The sequences were manually aligned using Se-Al v2.0a72 (Rambaut, 2001), with the criterion 'alignment as short as possible.' Another alignment (bidirectional, complementary; Gottschling et al., 2001; Coleman, 2003; Goertzen et al., 2003; Gottschling et al., in press) was investigated on the basis of a framework dictated by the secondary structure of the ITS1 transcript, with separate aligning of homologous regions. The complete data matrices are available in NEXUS format on request from the first author. Furthermore, *trn*L sequences have been checked for deletions and insertions in the alignment editor.

Parsimony analyses were performed using NONA 2.0 (Goloboff, 1993) and PAUP* 4.0b1 for Power Macintosh PC (Swofford, 1998). A distance procedure (neighbor-joining, with 2000 replicates; Kimura, 1980) was calculated with TREECON (van de Peer & de Wachter, 1993). Searches for best trees and bootstrap analyses were the same as in Gottschling and Hilger (2001): Bootstrap re-sampling (Felsenstein, 1985) was performed with 1000 replicates and a heuristic search with the following settings: addseq = random, nreps = 100, and mulpars = off for each bootstrap replicate. Gaps were considered as informative and calculated as a fifth base (since otherwise the information from secondary structure is lost). Molecular results were compared to morphological data accomplished from field observations, studies of herbarium specimens, and the literature.

Results

Analyses of the ITS1 data with NONA, PAUP*, and TREECON yield trees with similar major topologies in both parsimony searches and neighbor-joining. Parsimony searches (PAUP) yielded 1031 shortest trees with L = 680 (CI: 0.551, RI: 0.791) using a regular alignment with the criterion 'as short as possible' (285 bases in length) and 9853 shortest trees with L = 796 (CI: 0.513, RI: 0.778) using an alignment based on the secondary structure of the ITS1 transcript (307 bases in length, both not shown). While the major topologies do not differ between different programs and methods, the bootstrap support values vary using different alignments and methods.

Figure 1 shows a distance tree (TREECON) of *Cordia* and its allies with bootstrap support values from neighbor-joining (above branches: regular alignment/below branches: secondary structure alignment). *Coldenia procumbens* does not cluster with *Ehretia tinifolia* (both Ehretiaceae), but is closely allied to Cordiaceae (86/96 bootstrap support values). However, all Cordiaceae constitute a monophyletic group compared to outgroup representatives (94/63 bootstrap support values) and segregate into four monophyletic assemblages, with *Auxemma*, *Patagonula*, and *Saccellium* nested in *Cordia*:

1. The Varronia clade (currently recognized as *Cordia* sect. *Varronia*), with an exclusive New World distribution, is monophyletic (100/100 bootstrap support values) and is poorly resolved. Only the three species characterized by spicate inflores-

Table 1. Species list. DNA numbers follow an internal numbering code of the Institut für Biologie–Systematische Botanik und Pflanzengeographie (FU Berlin). Abbreviations: EHR: Ehretiaceae; EUC: *Cordia* sect. *Cordia*; GER: *Cordia* sect. *Gerascanthus*; HB: Botanical Garden; HEL: Heliotropiaceae; MYX: *Cordia* sect. *Myxa*; PHY: *Cordia* sect. *Physoclada* (i.e., *C. nodosa*); PIL: *Cordia* sect. *Pilicordia*; RHA: *Cordia* sect. *Rhabdocalyx*; SUP: *Cordia* sect. *Superbiflorae*; VAR: *Cordia* sect. *Varronia*.

DNA No.	Species name with author	Classification	*Collector/collection #* (herbarium)	Location (State)	GenBank No.
Cordiaceae					
1261	*Auxemma oncocalyx* (Allemão) Baill.	—	*Nunes s.n.* (MO)	Brazil	AY321592
1260	*Auxemma glazioviana* Taub.	—	*Quintana et al. 604* (PY)	Paraguay	AY321593
930	*Cordia africana* Lam.	MYX	*Pope 284* (B)	Zimbabwe	AY176067
371	*Cordia alliodora* (Ruíz & Pav.) Oken	GER	*HB Marburg* (BSB)	sine loc. [originally New World]	AY321594
1004	*Cordia angustifolia* (H. West ex Willd.) Roem. & Schult.	VAR	*Hilger 99/46* (BSB)	Cuba	AY321619
976	*Cordia aspera* G. Forst. f.	PIL	*Whistler 3113* (B)	Samoa	AY321595
262	*Cordia bifurcata* Roem. & Schult.	VAR	*Mehltreter ARG s.n.* (BSB)	Argentina	AF402575
56	*Cordia bonplandii* (Desv.) Roem. & Schult.	VAR	*HB Munich* (BSB)	sine loc. [originally New World]	AY321620
1206	*Cordia bordasii* A. Shinini	EUC	*Mereles & Degen 5513* (MO)	Paraguay	AY321596
1185	*Cordia borinquensis* Urb.	PIL	*Miller et al. 6596* (MO)	Puerto Rico	AY321597
915	*Cordia bullata* (L.) Roem. & Schult.	VAR	*Gottschling CUB 49* (BSB)	Cuba	AY176084
865	*Cordia cochinchinensis* Gagnep.	MYX	*in Chinese character 002245* (KUN)	China	AY321598
1072	*Cordia collococca* L.	PIL	*Miller & Sherman 6370* (BSB)	Mexico	AY176068
917	*Cordia curassavica* (Jacq.) Roem. & Shult.	VAR	*Wilbur 7631* (B)	Dominican Republic	AY321621
1205	*Cordia decandra* Hook. & Arn.	EUC	*Taylor et al. 10825* (MO)	Chile	AY321599
929	*Cordia dentata* Poir.	MYX	*Narvaez & Seymour 2527* (B)	Nicaragua	AY176069
384	*Cordia ecalyculata* Vell.	PIL	*Anonymous 5* (BSB)	Paraguay	AY321600
931	*Cordia elaeagnoides* DC.	RHA	*Miller & Tellez 3087* (BSB)	Mexico	AY321601
577	*Cordia elliptica* Sw.	PIL	*Gottschling CUB15* (BSB)	Cuba	AY321602
818	*Cordia faulknerae* Verdc.	MYX	*Medley 272* (MO)	Kenya	AY321603
909	*Cordia galleottiana* A. Rich.	EUC	*Gottschling CUB 38* (BSB)	Cuba	AY321604
918	*Cordia gharaf* (Forsk.) Ehrenb. ex Aschers.	MYX	*Greuter 20310* (B)	Namibia	AY176073
397	*Cordia guineensis* Thonn.	MYX	*HB Berlin-Dahlem 003-90-77-13* (BSB)	East Africa	AY321605
1196	*Cordia iguaguana* I. M. Johnst.	RHA	*Gentry et al. 37700* (MO)	Peru	AY321606
978	*Cordia lauta* I. M. Johnst.	VAR	*Miller & Tellez 3158* (BSB)	Mexico	AY321622
421	*Cordia lenis* Alain	VAR	*Hilger 18* (BSB)	Cuba	AF402577
1009	*Cordia leucocephala* Moric.	VAR	*Forstreuter 93170* (BSB)	Brazil	AY321623
1005	*Cordia lima* (Desv.) Roem. & Schult.	VAR	*Miller et al. 6572* (BSB)	Puerto Rico	AY321624
503	*Cordia longipedunculata* (Britt. & P. Wils.) Urb.	VAR	*Stenzel 802* (BSB)	Cuba	AY326125
988	*Cordia lutea* Lam.	MYX	*Weigend et al. 2000/707* (BSB)	Peru	AY176070
1199	*Cordia mairei* Humbert	MYX	*Miller & Miller 3796* (MO)	Madagascar	AY321607
396	*Cordia monoica* Roxb.	MYX	*HB Berlin-Dahlem 084-19-83-53* (BSB)	Zimbabwe	AY176071
1006	*Cordia morelosana* Standl.	GER	*Miller & Tenorio 565* (BSB)	Mexico	AY321608
377	*Cordia myxa* L.	MYX	*HB Berlin-Dahlem* (BSB)	sine loc. [originally Old World]	AF402578
939	*Cordia nodosa* Lam.	PHY	*Weigend et al. 5742* (BSB)	Peru	AY176072
1007	*Cordia panamensis* L. Riley	PIL	*Miller & Miller 1000* (BSB)	Panama	AY321609

Table 1. Continued.

DNA No.	Species name with author	Classification	*Collector/collection* # (herbarium)	Location (State)	GenBank No.
1197	*Cordia parvifolia* A. DC.	RHA	*Diggs & Nees 3117* (MO)	Mexico	AY321610
1202	*Cordia rufescens* A. DC.	SUP	*Almeide 50050* (MO)	Brazil	AY321611
541	*Cordia sebestena* L.	EUC	*Gottschling CUB 48* (BSB)	Cuba	AF385773
982	*Cordia seleriana* Fernald	EUC	*Miller & Tenorio 510* (BSB)	Mexico	AY321612
931	*Cordia sinensis* Lam.	MYX	*Breckle 3999* (B)	Israel	AY321613
979	*Cordia sonorae* N. E. Rose	GER	*Miller & Campos 2956* (BSB)	Mexico	AY321614
367	*Cordia subcordata* Lam.	EUC	*HB Berlin-Dahlem 162-62-87-10* (BSB)	Papua New Guinea	AF385774
1204	*Cordia superba* Cham.	SUP	*Souza s.n.* (MO)	Brazil	AY321615
1203	*Cordia taguahyensis* Vell.	SUP	*Thomas et al. s.n.* (MO)	Brazil	AY321616
118	*Cordia trichotoma* Vell. ex Steud.	GER	*Hilger et al. ARG 95/58* (BSB)	Argentina	AF402580
1200	*Cordia varronifolia* I. M. Johnst.	RHA	*Hutchinson & Wright 6774* (MO)	Peru	AY321617
916	*Patagonula americana* L.	—	*HB Munich* (BSB)	Argentina	AY176080
1198	*Patagonula bahiensis* Moric.	—	*Souza 5395* (MO)	Brazil	AY321618
815	*Saccellium lanceolatum* Humb. & Bonpl.	—	*Taylor 11353* (MO)	Argentina	AF402592
Ehretiaceae					
977	*Coldenia procumbens* L.	EHR	*Bean 13638* (B)	Australia	AY321591
439	*Ehretia tinifolia* L.	EHR	*Gottschling CUB 52* (BSB)	Cuba	AF385793
Heliotropiaceae					
686	*Tournefortia microcalyx* (Ruíz & Pav.) I. M. Johnst	HEL	*Weigend & Dostert 97/5* (BSB)	Peru	AF396905

cences (*C. curassavica, C. lenis, C. angustifolia*) are clearly retrieved as monophyletic (98/99 bootstrap support values). There are not enough species included to recognize the relationships of other subordinate taxa.

2. The Sebestena clade (57/82 bootstrap support values), with a mostly New World distribution (only *C. subcordata* from the Old World), includes *Cordia* sects. *Cordia* and *Gerascanthus*, three species of *Cordia* sect. *Rhabdocalyx*, and the three taxa *Auxemma, Patagonula,* and *Saccellium* that were formerly segregated from *Cordia*. The Sebestena subclade itself is not well resolved. Neither *Cordia* sects. *Gerascanthus* nor *Rhabdocalyx* (excluding *C. varronifolia*) seem to be monophyletic assemblages, but together they have poor or moderate bootstrap support (52/67 bootstrap support values). Compared to the other clades, the branch lengths found in the Sebestena clade are relatively long (Fig. 1). The putatively close relationship of *Patagonula* and *Saccellium* has no support from the ITS1 data (Fig. 1), but can be inferred from *trn*L sequence data (Fig. 2): These taxa alone share a unique insertion of 5 bases.

3. The Collococcus clade (100/100 bootstrap support values), with a primarily New World distribution, comprises the New World species of *Cordia* sect. *Myxa* (including *Cordia* sects. *Pilicordia* and *Physoclada*) as well as *Cordia* sect. *Superbiflorae*. Furthermore, *C. varronifolia* (*Cordia* sect. *Rhabdocalyx*) nests within the strongly supported monophyletic group representing *Cordia* sect. *Superbiflorae* (96/100 bootstrap support values).

4. The Myxa clade (100/100 bootstrap support values), with a largely Old World distribution, comprises Old World species of *Cordia* sect. *Myxa* and two New World species, *C. lutea* and *C. dentata*. All Old World taxa constitute a poorly supported monophyletic group (63/55 bootstrap support values), respectively a well-supported clade (98/99 bootstrap support values) after the exclusion of a basal group comprising *C. africana* and *C. mairei*.

The relationships between the four main clades are reasonably supported by molecular data. The Varronia clade is the sister group of the remainder of all other ingroup taxa (89/96 bootstrap support values). The Sebestena clade appears to be the sister group of the clades Collococcus and Myxa; the close relationship of the latter is moderately supported (79/78 bootstrap support values).

There are informative differences in the length of helices I and IV of the secondary structure of the ITS1 transcript. Hairpin I is shorter in the Old World representatives of the Myxa clade (excluding

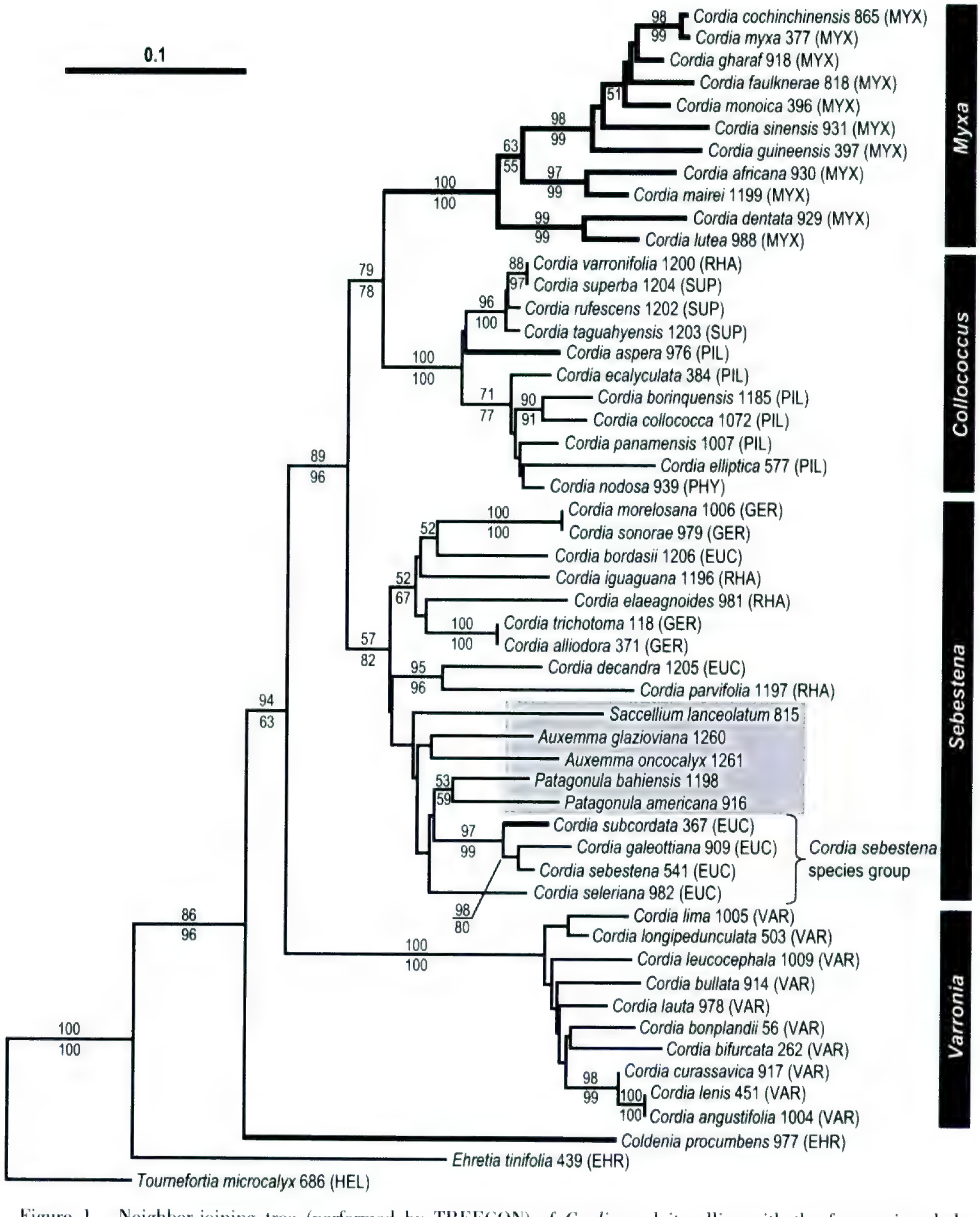

Figure 1. Neighbor-joining tree (performed by TREECON) of *Cordia* and its allies with the four major clades Varronia, Sebestena, Collococcus, and Myxa indicated. The numbers on the branches are bootstrap support values to the clusters to the right of them (above the branches: regular alignment, below the branches: secondary structure alignment; bootstrap support values under 50 not shown). The gray box indicates the taxa *Auxemma, Patagonula,* and *Saccellium* that were formerly separated from *Cordia.* Bold branches highlight Old World taxa, while New World taxa have thinner branches. DNA numbers and abbreviations for taxonomic assignments are the same as explained in the legend of Table 1.

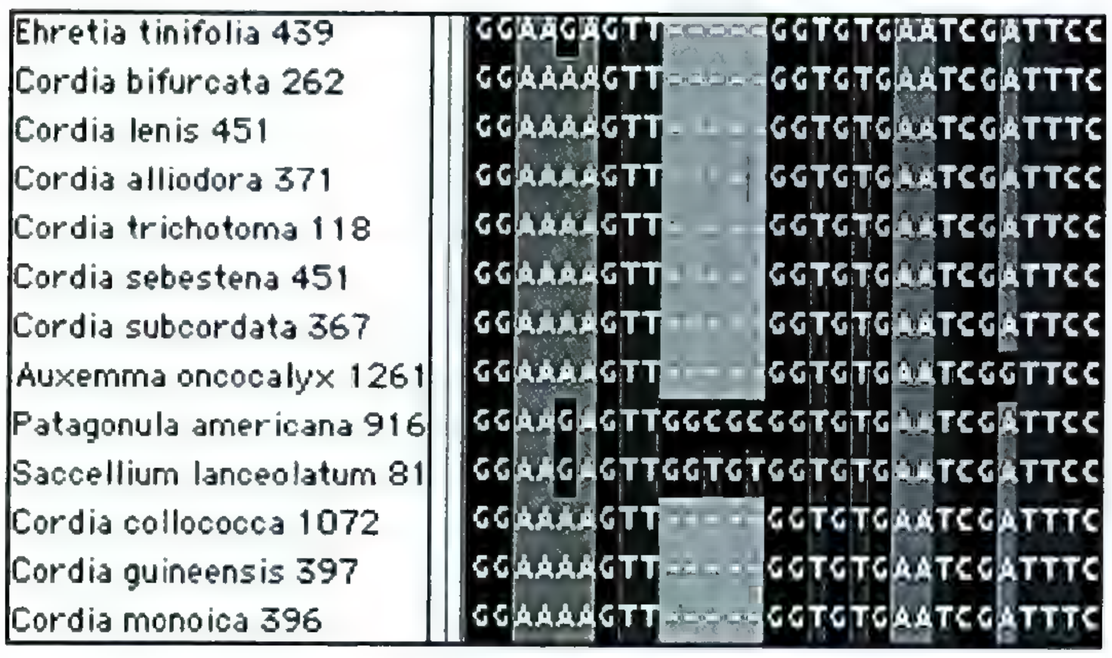

Figure 2. Alignment of selected *trn*L sequences of Cordiaceae (with *Ehretia tinifolia* as outgroup representative). Note the unique 5 bp insertion in *Patagonula* and *Saccellium*, while the *trn*L sequences of Cordiaceae are otherwise largely identical.

C. africana and *C. mairei*) as compared to all other taxa (from about 17 base pairings down through about 13, not shown). Furthermore, the conserved hairpin III is 5 bp long in the clades Sebestena and Varronia, 6 bp long in the clades Collococcus and Myxa.

Discussion

Plausibility of the Molecular Tree

Cordiaceae, as here circumscribed segregating into four clades, constitute a monophyletic group (94/63 bootstrap support values), which confirms a hypothesis that has been accepted by most previous authors (Candolle, 1845; Miers, 1875; Gürke, 1893; Miller, 1985). Johnston (1930, 1951), who worked on *Cordia* and its allies for over 25 years, emphasized the naturalness of the group, and the inclusion of *Saccellium* (traditionally Ehretiaceae) would be the only change from his circumscription of Cordiaceae. Furthermore, monotypic *Coldenia procumbens* does not cluster with *Ehretia tinifolia* (traditionally both Ehretiaceae), but appears to be more closely allied to Cordiaceae instead (86/96 bootstrap support values). Morphologically, *Coldenia* L. is decidedly unusual compared to other Cordiaceae, as it is an herbaceous annual (while all the other Cordiaceae are shrubs or trees), and it does not share the apomorphic traits of Cordiaceae as discussed below.

Flower and fruit anatomy support the monophyly of Cordiaceae as retrieved by molecular analysis (94/63 bootstrap support values). The drupe consists of a very hard to fibrous, undivided endocarp enclosing four or (by abortion) fewer seeds (Fig. 3A), a feature only sporadically found in other Boraginales (e.g., *Ehretia microphylla* Lam. of Ehretiaceae, *Heliotropium supinum* L. of Heliotropiaceae, species of *Rochelia* Rchb. of Boraginaceae s. str.). This undivided endocarp, derived from the four-parted endocarp found in the majority of Boraginales, and a twice-bifid style (Fig. 3B) are the most striking apomorphies of Cordiaceae (see also Table 2). Plicate cotyledons (Fig. 3C), another unique character within Boraginales, are doubtless apomorphic for Cordiaceae. This feature may be causally related to the loss of endosperm (functional substitute).

Four major clades can be recognized in *Cordia* on the basis of molecular data, which correspond to more or less established and species-rich taxonomic units as inferred from morphology, biogeog-

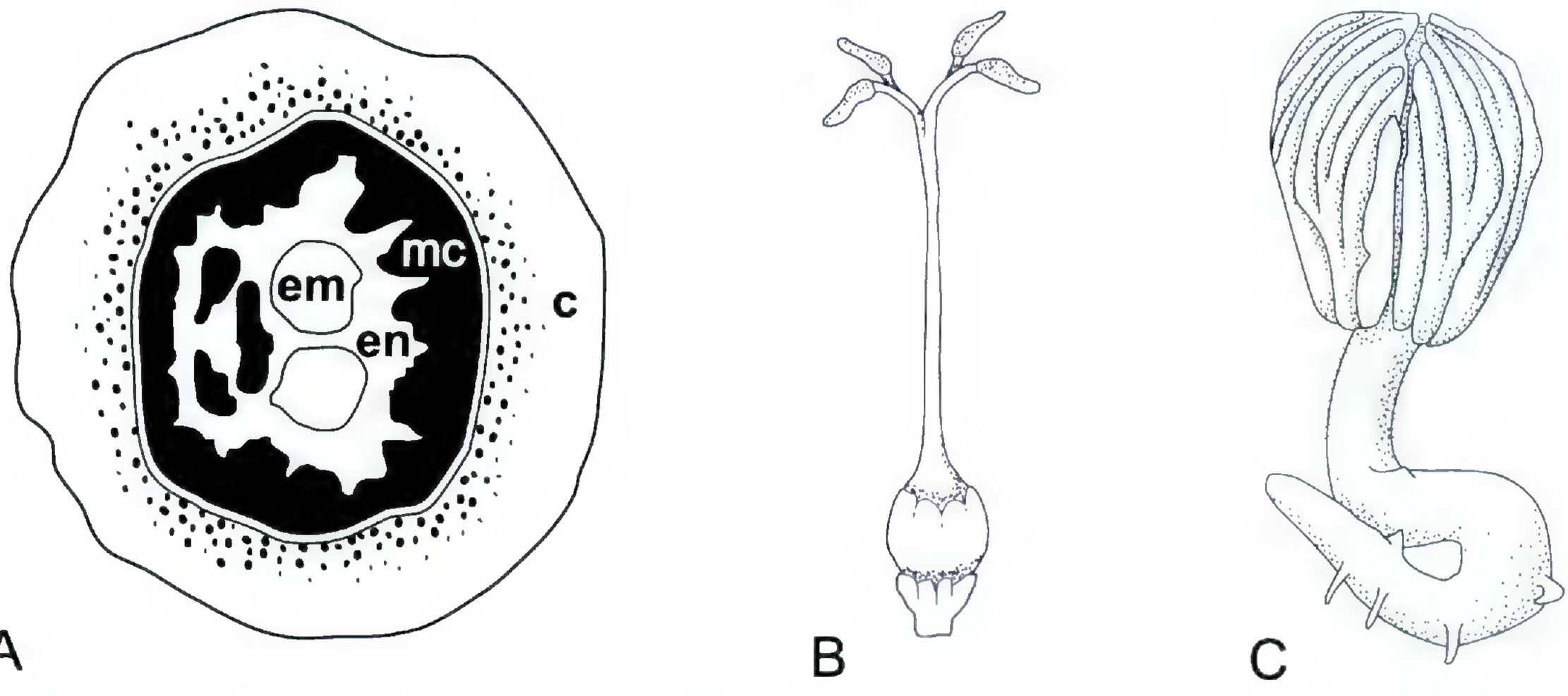

Figure 3. Apomorphies of Cordiaceae. —A. Fruit cross section of *C. sebestena* showing the undivided endocarp and the carnose calyx. —B. Style with four stigmatic lobes (*C. alliodora*). —C. seedling with plicate cotyledons (*C. dentata*). A redrawn from Tomlinson and Fawcett (1980); B and C redrawn from Gaviria (1987). Abbrevations: c: calyx; em: embryo; en: endocarp; mc: mesocarp.

Table 2. Character polarization in Cordiaceae, as inferred from phylogenetic hypotheses explained in the discussion. The numbers refer to the apomorphies indicated in the cladogram of Figure 6.

Number in Figure 6	Character	Apomorphy	Plesiomorphic condition
1	stigmatic lobes	four	two
2	endocarp	undivided	four-parted
3	cotyledons	plicate	flat
4	inflorescence architecture	syndesmic	thyrsoid
5	pollen	tri-porate	tri-colporate
6	syndesmia	spicate	cephaloid
7	distribution	colonizaton of Africa	New World
8	helix I of the ITS1 transcript	shortened	17 bp long
9	flowers	large (convergence to 15)	small
10	fruits	asymmetric (oblique)	symmetric (erect)
11	crystals in wood	prismatic	sand
12	drupe at maturity	enclosed in the calyx	free
13	exine	striate	spinulose
14	5 base insertion in *trn*L sequences	present	not present
15	flowers	large (convergence to 9)	small
16	calyx at fruit maturity	carnose	coriaceous
17	crystals in the wood	columnar	prismatic

raphy, and ecology: (1) Varronia (100/100 bootstrap support values; exclusively New World, approx. 100 species), (2) Collococcus (100/100 bootstrap support values; exclusively New World, approx. 100 species), (3) Myxa (100/100 bootstrap support values; predominantly Old World, approx. 50 species), with less support for (4) Sebestena (57/82 bootstrap support values; predominantly New World, approx. 50 species). This resolution is clearly an improvement, as compared to the numerous systematic concepts previously proposed for *Cordia* (e.g., Kuntze, 1891; Britton & Millspaugh, 1925; Friesen, 1933). Frequently, such concepts focused on the circumscription of well-recognizable species groups, with clear apomorphies, and relegated the remainder of such taxa to trash groups (e.g., *Gerascanthus* sensu Borhidi et al., 1988).

Varronia. The species of the Varronia clade are distinct in their morphology, distribution, and ecology, and their systematic segregation from the remainder of *Cordia* has been proposed consistently (Johnston, 1949; Taroda & Gibbs, 1986; Borhidi et al., 1988; Nowicke & Miller, 1990), which is now also strongly supported by molecular data from the ITS1 (Fig. 1).

Most representatives of Cordiaceae have thyrsoid inflorescences with monochasial or dichasial paracladia (i.e., lateral branches in compound inflores-

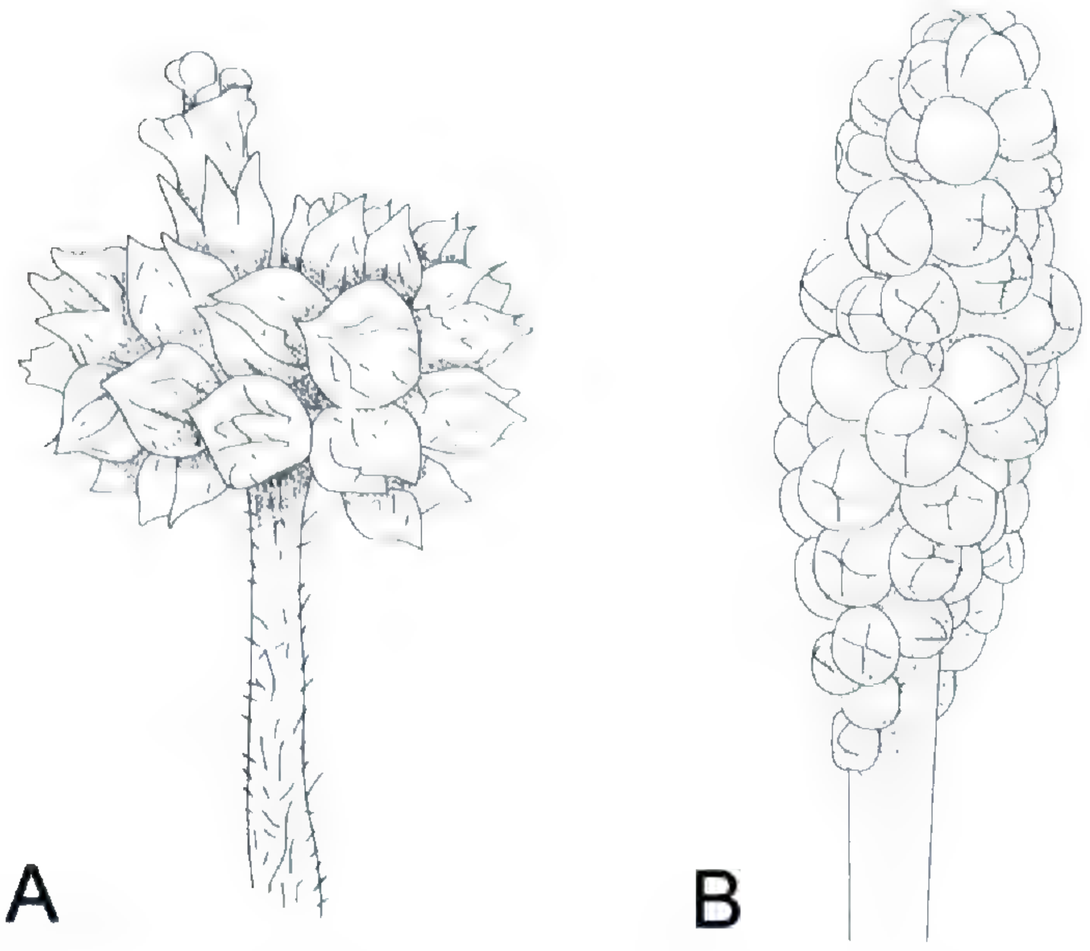

Figure 4. Syndesmia (Troll, 1964) found in Varronia (compare Uhlarz & Weberling, 1977). —A. Cephaloid-syndesmic inflorescence (*C. inermis* (Mill.) I. M. Johnst.). —B. Spicate-syndesmic inflorescence (*C. curassavica*). A redrawn from Nowicke (1969); B redrawn from Uhlarz and Weberling (1977).

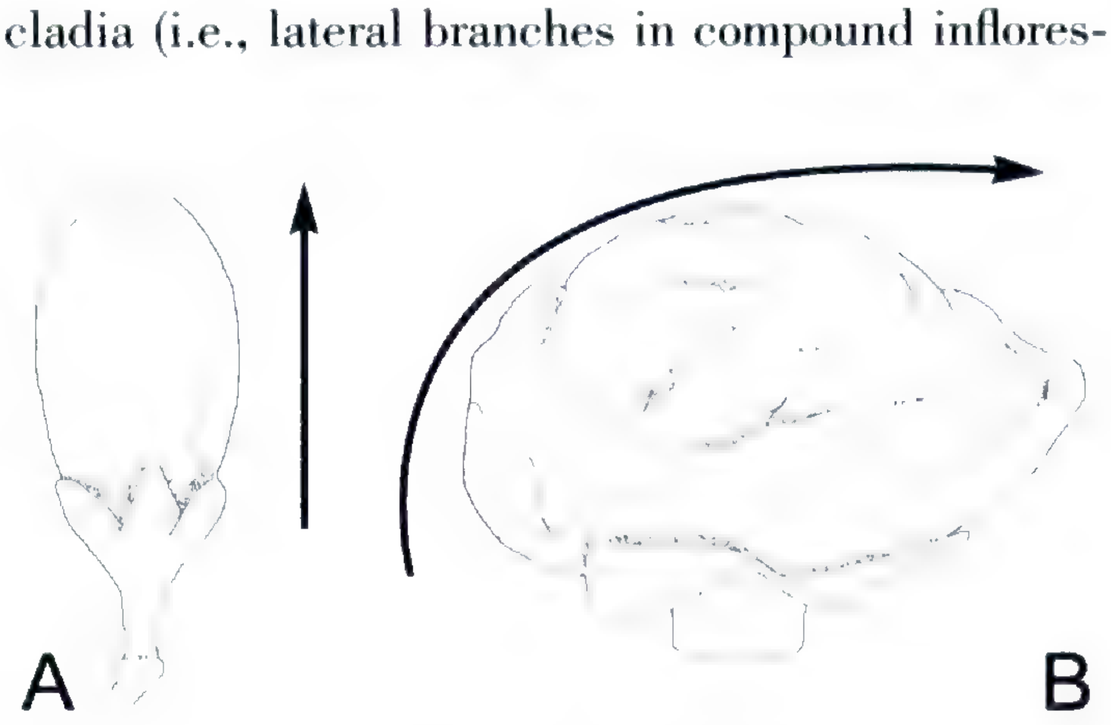

Figure 5. Fruit morphology. —A. Erect and symmetric fruit of *C. aspera.* —B. Obliquely transformed and asymmetric fruit of *C. collococca.* A redrawn from Kanehira (1936); B redrawn from Gaviria (1987).

cences repeating the structure of the main axis; Troll, 1964) that are also found in the outgroup (most Boraginales; plesiomorphic condition). However, syndesmia (i.e., partial inflorescences that are not freely developed, but are united with the main axis; Troll, 1964) have arisen in Varronia from thyrsoid inflorescences via complex developmental processes (Uhlarz & Weberling, 1977), leading to a doubling back of the inflorescence apex and the characteristic "disorderly" appearance of most Varronia inflorescences (older flowers are interspersed between young buds, flowering sequence is often acropetalous). Two types of syndesmia have been proposed that are distinguishable in early ontogeny, cephaloid and spicate (e.g., Gaviria, 1987; Fig. 4). Uhlarz and Weberling (1977) demonstrated that the spicate-syndesmic inflorescence can be derived from the cephaloid-syndesmic inflorescence. This character polarity is also retrieved by the molecular phylogeny herein (98/99 bootstrap support values for *C. curassavica*, *C. lenis*, and *C. angustifolia*, the representatives with spicate-syndesmic inflorescences). Therefore, the basic cephaloid-syndesmic inflorescence of the majority of Varronia may be regarded as apomorphic for the entire clade (100/100 bootstrap support values; see also Table 2).

Species of Varronia are also distinctive in their pollen morphology, a character that is otherwise diverse in Cordiaceae (Nowicke & Ridgway, 1973; Sahay, 1979; Borhidi et al., 1988; Heubl et al., 1990; Nowicke & Miller, 1990). The tri-porate pollen of Varronia (with spinulose exine, occasionally with reticulate muri) is doubtlessly apomorphic and clearly distinct from the (plesiomorphic) tri-colporate type of the majority of Cordiaceae, rendering additional support for the monophyly of Varronia.

Sebestena. The largest departure in relationships of species from the classification of Johnston (1930, 1951) supported by ITS1 data lie within the morphologically heterogeneous Sebestena clade. However, its internal phylogeny is only poorly resolved (which may be partly due to long-branch attraction). The alignment dictated by the framework of the ITS1 secondary structure model (Gottschling et al., 2001) increases bootstrap support for its monophyly (from 57 to 82 bootstrap support values), which includes *Cordia* sects. *Cordia* and *Gerascanthus*, three species of *Cordia* sect. *Rhabdocalyx*, and the three formerly segregated taxa *Auxemma*, *Patagonula*, and *Saccellium*. However, the hypothesis that *Cordia* sect. *Gerascanthus* is closely allied to the clades Collococcus and Myxa (Taroda & Gibbs, 1986; Borhidi et al., 1988) is not supported by molecular data (Fig. 1).

Because of their distinct fruiting calyces, *Auxemma* and *Patagonula* have always been maintained as taxa separate from *Cordia* by previous authors (Candolle, 1845; Gürke, 1893). Only Miers (1875) in his treatment "On the Auxemmeæ, . . ." associated *Auxemma*, *Patagonula*, and *Saccellium* with other taxa of the *Cordia sebestena* species group, but did not give further detail for relationships. Traditionally, *Saccellium* has been placed in Ehretiaceae because of the bifid style of *S. lanceolatum* Humb. & Bonpl. (vs. twice-bifid as in Cordiaceae). However, flowers of the other species in *Saccellium* are not known so far. Since *Auxemma*, *Patagonula*, and *Saccellium* share undivided endocarps and plicate cotyledons (partly observed by Candolle, 1845; Miers, 1875), which are here considered as apomorphic, morphology and molecular data are congruent with their placement in Cordiaceae (for *Saccellium* already demonstrated in Böhle & Hilger, 1997; Gottschling et al., 2001). Conversely, bifid styles represent the plesiomorphic condition in Boraginales, can therefore not be used to identify relationships, and result probably from a simple reversion in *S. lanceolatum*. The taxonomic inclusion of *Auxemma*, *Patagonula*, and *Saccellium* in *Cordia* has been proposed in Gottschling and Miller (in prep.).

After pollination, the young drupe is protected by the calyx in all species of Cordiaceae, and frequently an accrescent calyx completely encloses the mature drupe. The carnose calyx found in the *Cordia sebestena* species group (Fig. 3A), which may have an attractive function in fruit dispersal for animals such as birds and mammals, is unique in Boraginales and argues for the monophyly of the corresponding group. The mature drupes of *Auxemma* and *Saccellium* are completely enclosed by a strongly inflated, papery calyx, which differs from all other Cordiaceae fruits and has been the reason for their taxonomic separation. However, this similarity may be due to convergence since they are not sister groups: *Saccellium* is closely allied to *Patagonula*, with spreading, rotor-shaped calyx lobes on the drupe, as inferred from the apomorphic 5 bases long insertion found in *trn*L sequences (Fig. 2).

Reticulate and/or striate ornamentation of tri-colporate pollen is only found in an—at first glance heterogeneous—assemblage comprising the *Cordia sebestena* species group (including *C. seleriana*, *C. decandra*, and *C. parvifolia*) plus *Auxemma*, *Patagonula*, and *Saccellium* (Borhidi et al., 1988; Nowicke & Miller, 1990). This species group is also retrieved in the molecular tree (Fig. 1, but bootstrap support values under 50) that does, however, not confirm the ". . . separate generic status . . ." of

Auxemma and *Patagonula* from *Cordia* (Heubl et al., 1990: 129). Thus, reticulate exines represent probably the apomorphic condition (Table 2), but also *C. bordasii* has a rugulate ornamentation. Miller and Nowicke (1989) suggested a placement of this species in *Cordia* sect. *Cordia*, but this plausible hypothesis is not supported by ITS1 data (*C. bordasii* is nested with *Cordia* sect. *Gerascanthus*).

Heubl et al. (1990) distinguished several types of crystals in the wood of Cordiaceae. The presence of crystal sand in all taxa investigated indicates that this is the plesiomorphic condition. Additionally, prismatic crystals are found in the Sebestena clade (excluding the *Cordia sebestena* species group), and columnar crystals are present in the *Cordia sebestena* species group. Both these crystal types are currently only known from this monophyletic group in Boraginales. We consider both crystal types as homologous and as lending additional support to the monophyly of Sebestena (57/82 bootstrap support values, Fig. 1). The columnar crystals in the *C. sebestena* species group may be derived from the less complex prismatic crystals found in the remainder of the Sebestena clade (see also Table 2).

Collococcus and Myxa. Johnston (1930) proposed the most widely accepted comprehensive classification of New World species of *Cordia*, and the ITS1 data support many of his assumptions about relationships. The molecular tree (Fig. 1) suggests a sister-group relationship (79/78 bootstrap support values) of the exclusively New World Collococcus clade (100/100 bootstrap support values) consisting of *Cordia* sects. *Pilicordia* and *Physoclada* (Johnston, 1930) and *Superbiflorae* (Taroda & Gibbs, 1986) and the largely Old World Myxa clade (100/100 bootstrap support values) that Johnston (1951) included in a pantropical *Cordia* sect. *Myxa*. The disjunction present in the Myxa clade is considered as the result of a colonization event (from the New World to Africa) by long-distance dispersal because of endozoochoria (Gottschling et al., 2004).

Four remarkable species of the Myxa clade are on two basal branches in the molecular tree (Fig. 1). These include *C. dentata* (from Mexico through Central America and the West Indies to northern South America) and *C. lutea* (from western Ecuador, Peru, and the Marquesas Islands in Polynesia), and *C. africana* and *C. mairei* (both from Africa and Madagascar). The relationships of these four species are not clearly resolved by ITS1 data, but they share a set of morphological features that are unusual in *Cordia*, including striate calyces with irregular dehiscence and yellow corollas with crumpled aestivation. The decision whether such characters are symplesiomorphic in the Myxa clade or apomorphic for these four species cannot be made by this study.

As in many groups of angiosperms, corolla size is highly homoplasious. Most Cordiaceae (and outgroup representatives) have relatively small corollas (not exceeding 15 mm diam.), but species with large corollas (more than 20 mm diam.) are found in all four clades (e.g., *C. lauta* from Varronia, *C. mairei* from Myxa, the latter with flowers up to 10 cm long). However, there are only two species groups that have been characterized by large corollas (Johnston, 1930; Taroda & Gibbs, 1986; Miller & Nowicke, 1989), namely the *Cordia sebestena* species group (nested within the Sebestena clade) and *Cordia* sect. *Superbiflorae* (nested within the Collococcus clade). The molecular tree (Fig. 1) confirms Taroda and Gibbs's (1986) assertion that these two groups are not closely related. Thus, large corollas result from convergent developments in Cordiaceae, but may be regarded as apomorphic for *Cordia* sect. *Superbiflorae* (96/95 bootstrap support values) and the *Cordia sebestena* species group, respectively (see also Table 2).

The reduction of the number of functional seeds per fruit sporadically occurs in Boraginales and is relatively common in Cordiaceae (and might be causally related to the formation of an undivided endocarp). In the majority of, but not all, species of Collococcus (e.g., *C. collococca, C. elliptica, C. nodosa*), the fruit becomes asymmetrical during ontogeny (Fig. 5) due to abortion of three of four ovules. This feature is occasionally found in other Boraginales (e.g., *Caccinia* Savi and *Trichodesma* R. Br. of Boraginaceae s. str.), but not in other Cordiaceae and this may be regarded as apomorphic for the species group within the Collococcus clade (71/77 bootstrap support values).

Investigations on secondary structures can be a useful tool for recognizing homologous base pairings (e.g., Coleman et al., 1998; Gottschling et al., 2001; Coleman, 2003; Gottschling & Plötner, 2004), and length variation of helices may be included in phylogenetic analyses (e.g., in Heliotropiaceae: Gottschling et al., 2001; Hilger & Diane, 2004). In Cordiaceae, such variations are found in hairpins IV, III, and especially hairpin I, while hairpin II remains highly conserved. The usual length of hairpin I is 17 bp (plesiomorphic condition, found in most investigated sequences), while in the Old World species of the Myxa clade (excluding *C. africana* and *C. mairei*) it is reduced to approximately 13 bp (apomorphic).

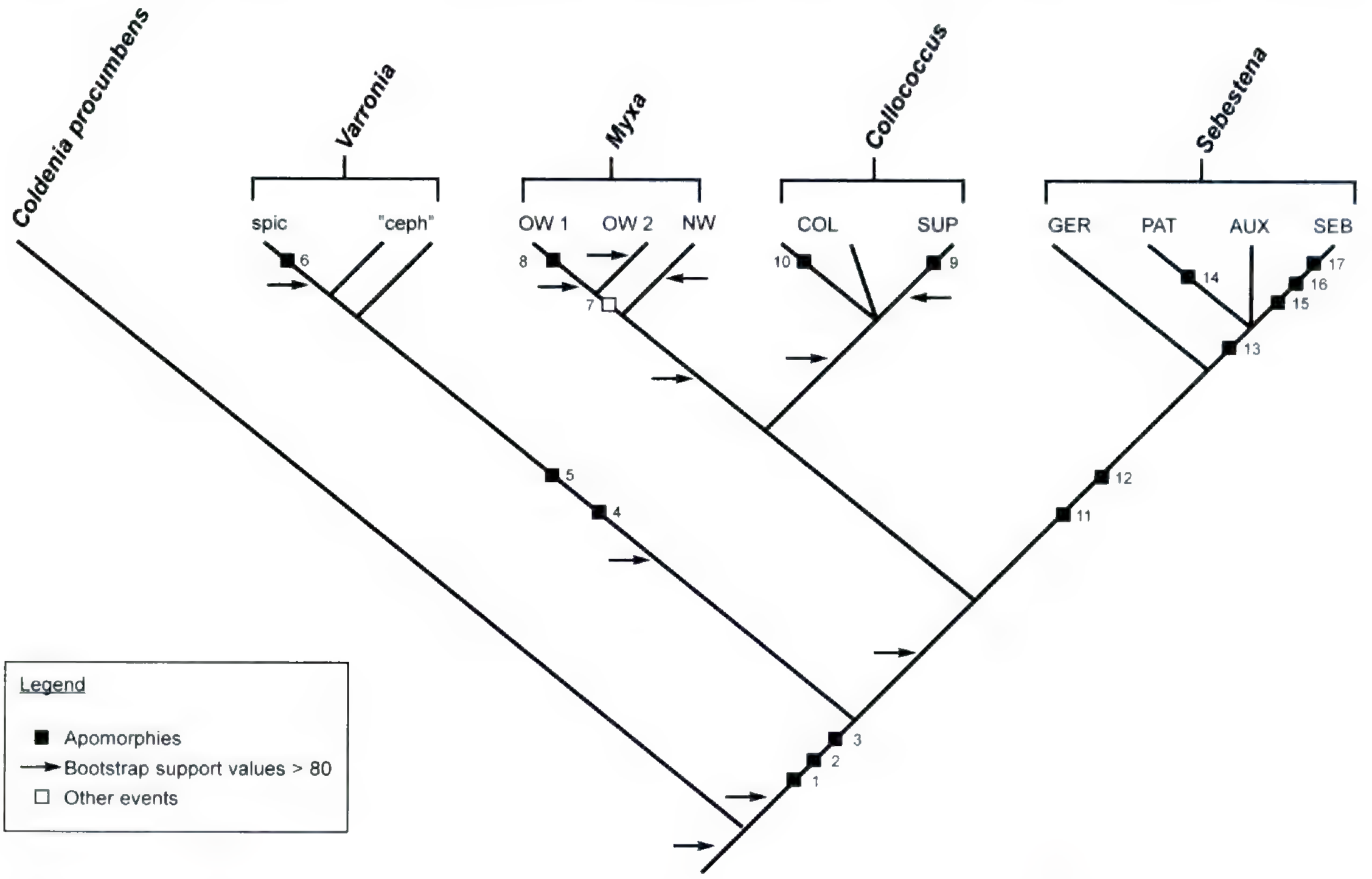

Figure 6. Annotated phylogram of Cordiaceae; apomorphies are listed in Table 2. Abbreviated taxa include: spic: Varronia species with spicate-syndesmic inflorescences (*C. angustifolia, C. curassavica, C. lenis*); "ceph": Varronia species with capitate-syndesmic inflorescences (*C. bifurcata, C. bonplandii, C. bullata, C. lauta, C. leucocephala, C. lima, C. longipedunculata*); OW1: Old World species group 1 of the Myxa clade (*C. cochinchinensis, C. faulknerae, C. gharaf, C. guineensis, C. monoica, C. myxa, C. sinensis*); OW2: Old World species group 2 of the Myxa clade (*C. africana, C. mairei*); NW: New World species of the Myxa clade (*C. dentata, C. lutea*); COL: remainder of the Collococcus clade when *Cordia* sect. *Superbiflorae* is excluded (*C. aspera, C. borinquensis, C. collococca, C. ecalyculata, C. elliptica, C. nodosa, C. panamensis*); SUP: *Cordia* sect. *Superbiflorae* (*C. rufescens, C. superba, C. taguahyensis*, including *C. varronifolia* from *Cordia* sect. *Rhabdocalyx*); GER: species group comprising *Cordia* sect. *Gerascanthus* (*C. alliodora, C. morelosana, C. sonorae, C. trichotoma*) and species of *Cordia* sects. *Cordia* (*C. bordasii*) and *Rhabdocalyx* (*C. elaeagnoides, C. iguaguana*); PAT: species of *Patagonula* (*P. americana, P. bahiensis*) and *Saccellium* (*S. lanceolatum*); AUX (*Auxemma glazioviana, A. oncocalyx*); SEB: *Cordia sebestena* species group (*C. decandra, C. galeottiana, C. sebestena, C. seleriana, C. subcordata*, including *C. parvifolia* from *Cordia* sect. *Rhabdocalyx*).

Conclusion

The cladogram in Figure 6 summarizes the results of this study. Morphological apomorphies, geographic separation, and other events are indicated together with significant bootstrap support values (> 80) from the molecular phylogeny (Fig. 1). The subordinate taxa of Cordiaceae, Varronia, Myxa, Collococcus, and Sebestena, are indicated.

A set of characters for the last common ancestor of Cordiaceae as deduced from the cladogram would include: woody habit, small trees or shrubs; phyllotaxis alternate; leaves undivided, obovate, estipulate, margins entire; flowers bisexual, calyx valvate, enclosing the drupe at least in early ontogeny, persisting in mature fruits; corolla sympetalous, tube short, lobes spreading; stamens included; style with four capitate stigmas (apomorphic for Cordiaceae); pollen tri-colporate, exine spinulose; fruits with a multilayered endocarp that is undivided (apomorphic for Cordiaceae) and has some irregular ridges on the outer surface; exocarp brightly colored (endozoochoria); seeds lacking endosperm (possibly apomorphic for Cordiaceae); cotyledons plicate (apomorphic for Cordiaceae). The last common ancestor of Cordiaceae may have lived in tropical climates in the Upper Cretaceous in the western part of the Gondwana continent (Gottschling et al., 2004). These character states of monophyletic Cordiaceae can now be used for further phylogenetic studies in Boraginales.

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PHOTOSYNTHATE CONTRIBUTION BY SEPALS ALLEVIATES THE CARBON COST OF REPRODUCTION IN THE SPRING EPHEMERAL *FLOERKEA PROSERPINACOIDES* (LIMNANTHACEAE)[1]

Ines Ben Mokhtar and Gilles Houle[2]

Abstract

Previous studies have shown that reproductive structures do not simply represent carbon sinks, since several flower parts are green and a fraction of the carbon allocated to reproduction may be obtained through the photosynthetic activity of these accessory structures. This extra-foliar contribution may represent up to 60% of the cost of production and maintenance of the reproductive structures. In *Floerkea proserpinacoides* (Limnanthaceae), a spring ephemeral annual plant of the deciduous forests of eastern North America, fruit maturation is costly and occurs only at the end of the plant's cycle. Sepals increase three- to five-fold in area after anthesis and thus may contribute significantly to the plant's carbon budget, thereby reducing the cost of reproduction. To test this hypothesis, plants were grown in shade and in full-light conditions, with sepals intact or removed. Results indicate that sepal contribution to the plant's carbon budget is more important in full light than in shade. In shade, sepals contribute 11% of the total biomass and 30% of the fruit output, while in full light they contribute 31% and 53% of the total biomass and fruit output, respectively. In *F. proserpinacoides*, each individual produces an average of only ca. three fruits per plant in the natural habitat at the margin of the species range in Québec. Hence, sepal contribution to the carbon budget may allow the plant to optimize its reproductive output in the relatively short temporal window that corresponds to the period prior to canopy closure.

Key words: accessory structures, carbon sink, costs of reproduction, extra-foliar carbon contribution.

Reproduction not only implies the production of flowers and fruits, but also of various ancillary structures and the loss of carbon through reproductive tissue respiration (Bazzaz & Reekie, 1987). Investment in current reproduction, which may be significant, typically occurs at the expense of growth, defense, survival, and/or future reproduction (Obeso, 2002). For instance, high reproductive investment in some tropical palms may be followed by increased risk of mortality (Oyama & Dirzo, 1988). However, reproductive investment varies with species: annuals and monocarpic perennials, which reproduce once in a lifetime, typically have a higher reproductive allocation than iteroparous perennials, which have multiple cycles of reproduction (Bazzaz et al., 1987).

In monocarpic plants, reproduction is often associated with a decrease of growth rate and/or an increase of death probability, considering that water, carbon, and minerals are diverted mostly toward the reproductive structures (Silvertown & Charlesworth, 2001). However, several factors may contribute to diminish the conflicts among functions, such as abundance of resources in the environment, photosynthetic activity of reproductive structures, sink-driven carbon assimilation and uptake of nutriments, and temporal segregation of reproduction and growth (Houle, 2001).

Temporal segregation may attenuate conflicts between growth and reproduction (Cohen, 1971; Paltridge & Denholm, 1974), since resource allocation occurs sequentially through time, and thus these functions do not create simultaneous demands for the same resources. Indeed, under these circumstances the uptake of nutrients and the absorption of carbon are first used for plant growth, reproduction being induced afterward. Examples of perennial plants showing temporal segregation of functions are species of *Solidago* L. and *Aster* L. (Asteraceae), mostly perennial plants of abandoned fields and forests (Marie-Victorin, 1995): several species of these two genera are characterized by a

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[2] Département de biologie, Université Laval, Sainte-Foy, Québec, Canada G1K 7P4. gilles.houle@bio.ulaval.ca.

vegetative growth period that may last up to four months, followed by a short reproductive period that is limited to a few weeks (Schmid et al., 1995; Walck et al., 2001). Aerial parts of those plants then die, whereas belowground parts formed by rhizomes continue, year after year, to develop new reproductive shoots. In annual plants such as *Impatiens* L. (Balsaminaceae) of both forest and open habitats in North America, there is also a temporal separation of growth and reproduction (Schoen et al., 1994).

Apart from the temporal segregation of reproduction and growth, the photosynthetic activity of reproductive structures can also attenuate internal conflicts. Indeed, although leaves are considered the main source of carbon (Guido & Hardy, 2003), reproductive structures do not simply represent carbon sinks since several flower parts are green and a fraction of the carbon allocated to reproduction may be obtained through the photosynthetic activity of these accessory parts (Bazzaz & Carlson, 1979a, b; Watson & Casper, 1984; Williams et al., 1985; Ogawa et al., 1995; McDowell et al., 2000). In certain cases, green accessory reproductive structures are capable of sufficient photosynthetic activity to assure a major fraction of the total carbon and energy needed for reproduction: for instance, flowers of *Acer platanoides* L. (Aceraceae) are responsible for ca. 65% of the total carbon required for reproduction (Guido & Hardy, 2003). This suggests that fruits and flowers should not be considered simplistically as a charge at the expense of the other parts of the plant (Bazzaz & Carlson, 1979a, b). However, it is not always obvious what structures or activities should be designated as reproductive (Bazzaz & Reekie, 1987).

For instance, in *Floerkea proserpinacoides* Willd. (Limnanthaceae), a small annual plant of the deciduous forests of eastern North America, sepal surface area increases as the plant grows and continues to flower. We hypothesize that sepals are involved in the reduction of the reproductive costs of this ephemeral plant. On the basis of previous studies, which showed that reproductive structures in some species can contribute up to 60% of the total carbon needed for reproduction (Watson & Casper, 1984), we determined if sepals of *F. proserpinacoides* contribute significantly to the carbon needed by the developing fruits.

Study Species

Floerkea proserpinacoides is a spring ephemeral annual plant, ranging in eastern North America from West Virginia, North Carolina, Tennessee, and Missouri to Ontario, Québec, and Nova Scotia (Fernald, 1950; Steyermark, 1963; Gleason & Cronquist, 1991). In Québec, where the species reaches the northern limit of its distribution, *F. proserpinacoides* is mainly limited to humid and rich forests, on islands of the Saint-Lawrence River (McKenna & Houle, 2000b).

Seed germination begins in late fall and early winter (November–January; Baskin et al., 1988; Houle et al., 1998), but seedlings do not emerge until the following spring. The first leaves expand at the end of March, at a time when snow is still present on the ground in southern Québec (at our study site). Flowering is initiated after ca. 2–3 weeks of growth and continues through early June (Houle, 2002). Seeds are disseminated at the end of June. Senescence occurs after approximately 60–70 d of growth (Struik, 1965) and coincides with an increase in environmental temperatures and a decrease in irradiance due to canopy closure (Struik, 1965; McKenna & Houle, 2000a).

Floerkea proserpinacoides produces small, autogamous flowers, one per node, except for the first two or three nodes at the base of the plant (Ornduff & Crovello, 1968; Smith, 1983). Petals are very small, white, and caducous; however, sepals are green, persistent, and, after anthesis, become three to five times larger than their initial size. Each flower has one to three carpels and can produce one, two, or more rarely three nutlets (1.5–2.5 mm diam.), each containing a seed. At low densities (100 individuals m^{-2}) a plant can produce up to 12 nutlets (Smith, 1983), which is relatively few for an annual plant. However, at the northern limit of the species range in Québec, mean fecundity is only three nutlets per plant (Houle et al., 2001). Nutlets enlarge mostly near the end of the growth period, just before senescence.

Materials and Methods

In early August 2002, three 25 × 50 × 5 cm blocs of soil containing seeds of *Floerkea proserpinacoides* were collected from a population of this species at île aux Grues, Québec, Canada (47°02′N, 70°35′W). To break seed dormancy, seeds were first stored in a dry environment at ambient temperatures (20°C–25°C, for a period of 3 months) and subsequently in a moist environment at 5°C for 2 months. After this cold stratification period, the blocs were placed in a greenhouse for seedling emergence.

We selected 48 seedlings (2-leaf stage) from the three blocs, transplanted them into pots (10 × 10 × 9 cm) filled with sand, and watered them every

day with tap water and once a week with a nutrient solution (0.021 g N L^{-1}). After 3 weeks of growth, we placed an acetate tube (with small holes to allow for air circulation) over each plant to ensure collection of all fruits produced by the plant. Mean maximum and minimum temperatures in the greenhouse were then 25.0° and 12.7°C, respectively.

For the light factor, we installed 12 cages, each covered with a transparent plastic sheet (with small holes to allow for air circulation). These cages represented our control for light (full-light, FL), with a mean photosynthetic photon flux density (PPFD) of 202.3 μmol m^{-2} s^{-1}. Twelve other cages were covered with a sunshade (shade, S), since we hypothesized that the role of sepals in photosynthesis would be more evident if light was reduced (mean PPFD in these 12 cages was 113.2 μmol m^{-2} s^{-1}). The 24 cages were laid out in 12 blocks, each with one full-light cage and one shade cage. Each cage contained two pots, each with one plant.

The sepal-removal treatments were then applied. Each day, the sepals of sepal-removal plants were surgically removed, placed in small envelopes, and dried, while those of control plants were left intact. From the sixth week of growth onward, to simulate the closing of the forest canopy, we further reduced light in the shade cages by adding layers of sunshade (mean PPFD in these cages was then 59.2 μmol m^{-2} s^{-1}). Full-light cages were left with their initial transparent plastic sheet. We also increased the mean maximum and minimum temperatures in the greenhouse to 27.8° and 15.7°C, respectively, and modified the frequency of watering: plants were watered every 2 d and no fertilizer was applied. The end of the experiment was marked by plant senescence in the FL cages. After 8 weeks of growth (since transplantation), plants were separated into roots, stem, leaves, flowers, and fruits. All plant material was dried for 24 h at 75°C and then weighed. We also determined the total number of flowers and fruits (both mature and total) for each plant.

The experiment was carried out on the campus of Université Laval, Québec (Canada), from January through February 2003. The low solar angle during that period, the opacity of the greenhouse window panes, in combination with the opacity of the plastic sheets used to cover the full-light cages explain the relatively moderate PPFD values of the full-light treatment (compared with deciduous forest conditions in the spring, at a similar latitude). Nevertheless, PPFD levels were at least twice as high in the full-light cages as in the shaded cages and induced significant responses from the plants (see Results below).

Statistical Treatment

Differences between the full-light and shade treatments and between the sepal-removal and control treatments were tested in randomized complete block design ANOVAs, one for each variable: total biomass, number of flowers, number of fruits (total and mature), and four biomass ratios (reproductive ratio, REPR: reproductive biomass/total biomass; stem ratio, SR: stem mass/total biomass; leaf ratio, LR: leaf mass/total biomass; root ratio, RR: root mass/total biomass). REPR, SR, LR, and RR were arcsine-square-root transformed for the analyses.

Results

Sepal removal markedly decreased total plant biomass, particularly at high light levels (33.3% decrease in FL plants and 14.5% decrease in S plants; significant light × sepal removal interaction at $P = 0.0408$; Fig. 1). Differences in total biomass between control and sepal-removal plants cannot be accounted for solely by the mass of the sepals that was removed. Indeed, sepal mass was only 0.0050 g and 0.0041 g for FL and S plants (sepal-removal treatment), respectively, whereas differences in total biomass between control and sepal-removal plants was 0.0644 g in FL and 0.0165 g in S plants.

Sepal removal decreased the number of flowers (by 29.0% in FL plants and by 25.4% in S plants) and carpels (by 34.5% in FL plants and by 28.0% in S plants), independently of light level (Fig. 2). Number of mature fruits was also reduced by sepal removal, particularly at high light levels (52.5% reduction in FL plants and 13.0% reduction in S plants; significant light × sepal removal interaction at $P = 0.0021$; Fig. 2). When expressed in terms of mature fruit number per gram of leaf, the standardized reproductive output of sepal-removal plants was lower than that of control plants, particularly at high light levels (shade: 338 ± 46 and 447 ± 55 fruits g^{-1}, for sepal-removal and control plants, respectively; full light: 355 ± 42 and 604 ± 48 fruits g^{-1}, for sepal-removal and control plants, respectively; significant light × sepal removal interaction at $P = 0.0435$). The average number of mature fruits per mature flower did not differ between sepal-removal and control plants in shade (0.68 ± 0.12 and 0.58 ± 0.11, respectively). In the full-light treatment, however, control plants produced 38% more mature fruits per mature flower than sepal-removal plants (0.91 ± 0.08 and 0.66 ± 0.10, respectively; significant light × sepal removal interaction, $P = 0.0466$).

Of the four biomass ratios analyzed, only RR was

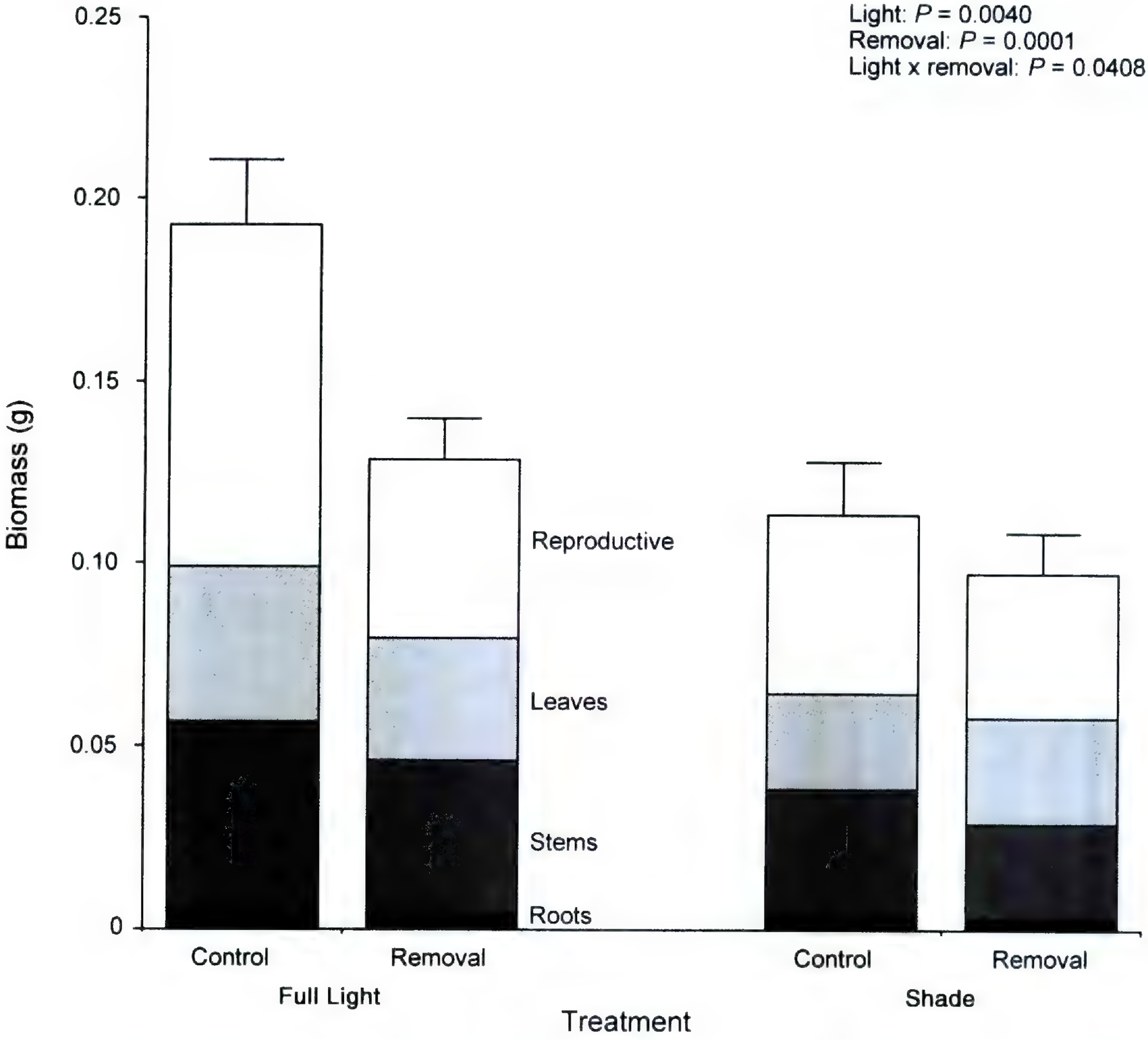
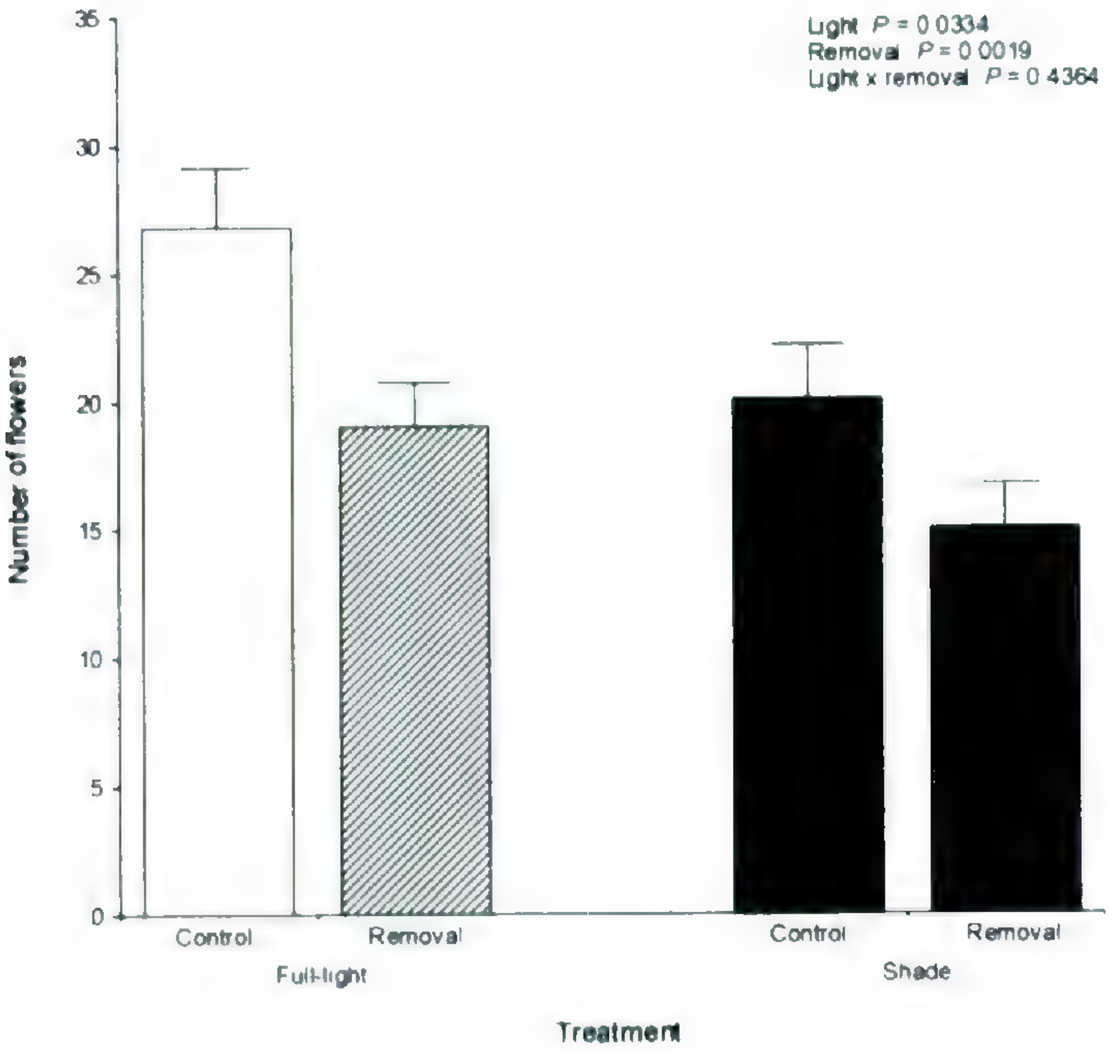


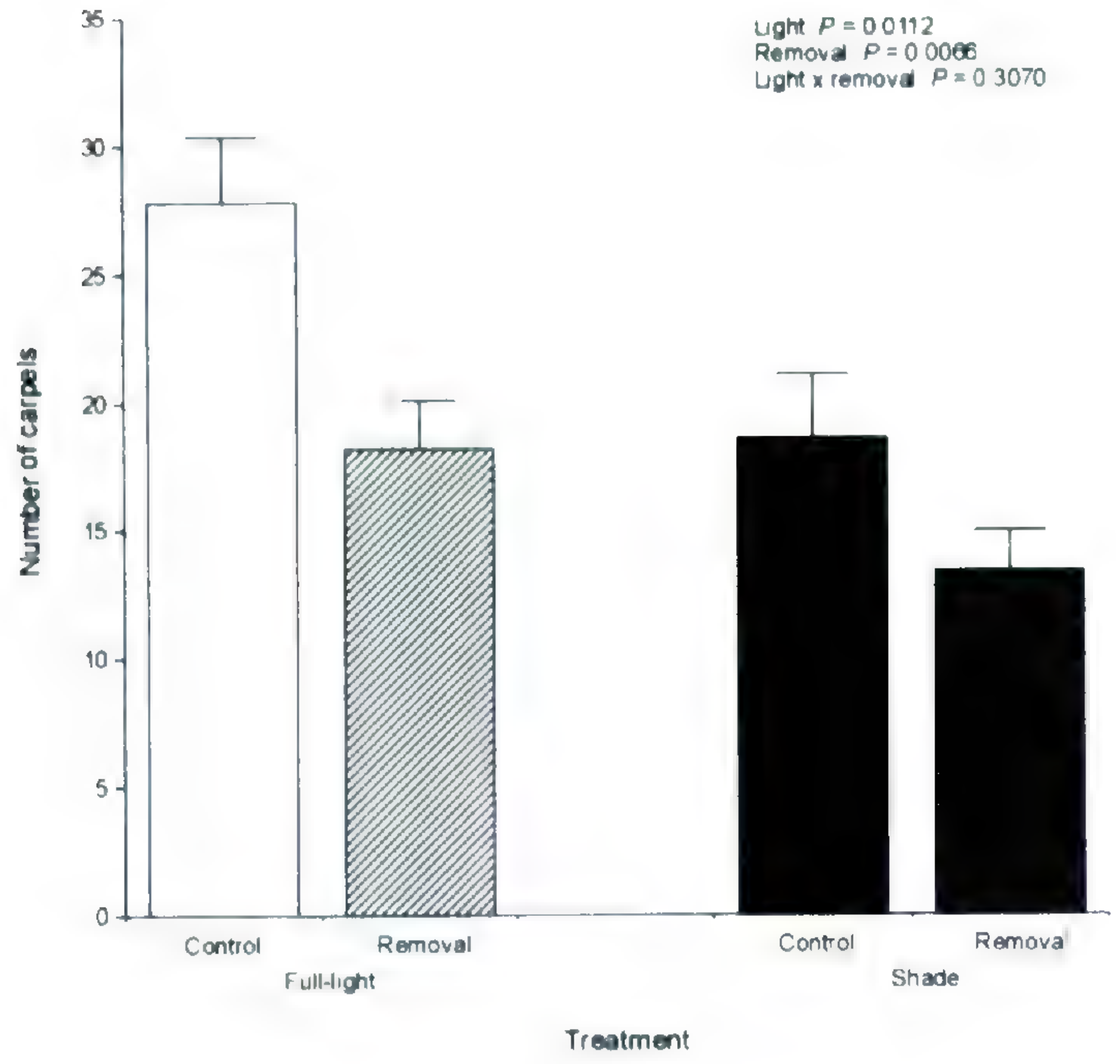
Figure 1. Effects of light level and sepal removal on total biomass (root, stem, leaf, and reproductive biomass) of *Floerkea proserpinacoides* (Limnanthaceae). Mean + 1 s.e. (N = 12). *P*-values for randomized complete block design ANOVA.

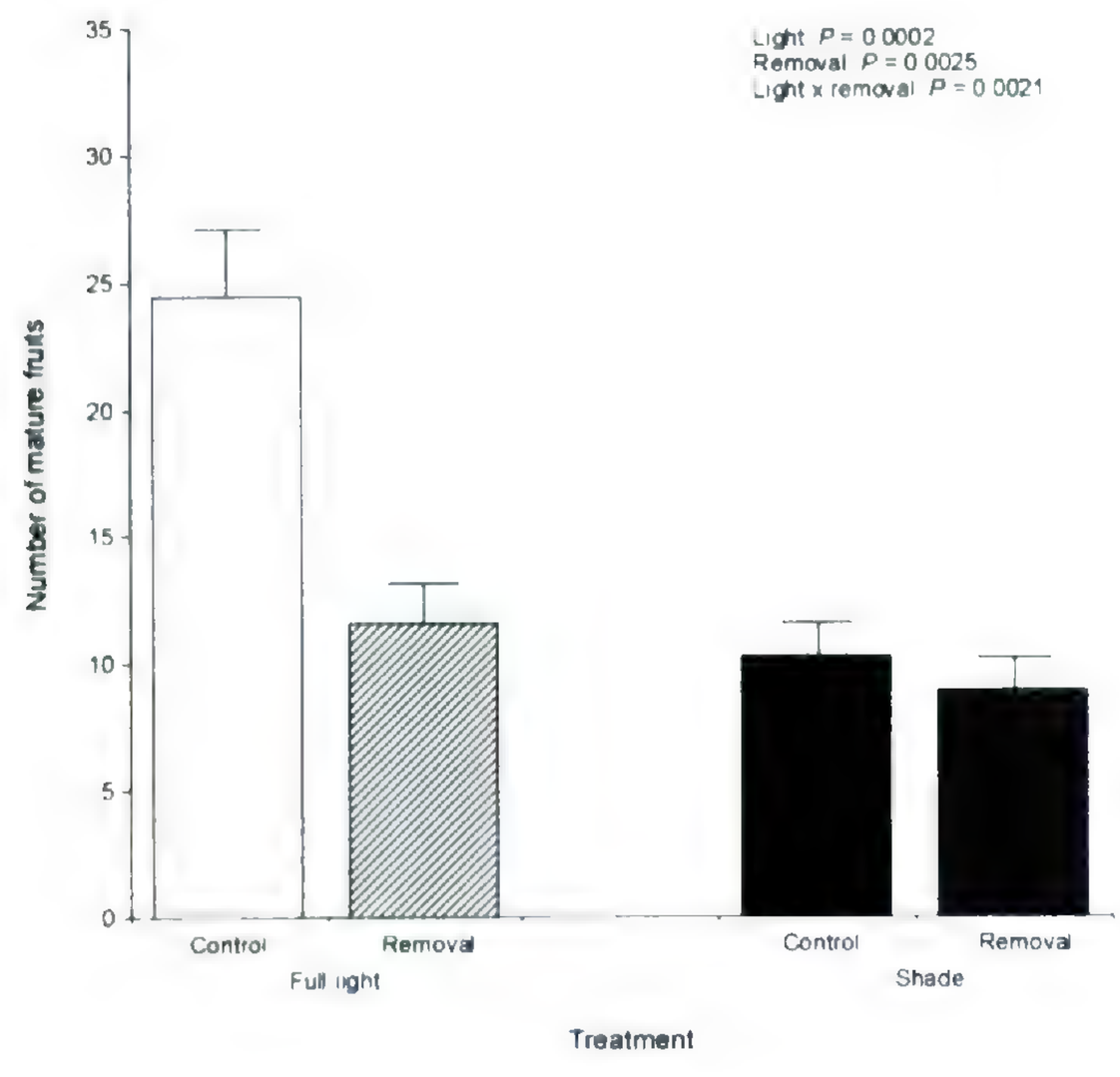
not affected by sepal removal ($P = 0.1321$; Table 1 and Fig. 1). SR increased as a response to sepal removal only in FL plants (26.6% increase vs. 7.8% increase in S plants; significant light × sepal removal interaction at $P = 0.0026$; Table 1 and Fig. 1). LR also increased as a result of sepal removal, but similarly in S (29.0%) and in FL plants (22.3%; $P = 0.0014$ for sepal removal, with no significant light × sepal removal interaction at $P = 0.6391$; Table 1 and Fig. 1). However, REPR decreased in response to sepal removal, particularly at high light levels (36.0% decrease for FL plants and 10.3% decrease for S plants; significant light × sepal removal interaction at $P = 0.0366$; Table 1 and Fig. 1). Light level alone had no significant effect on any of the biomass ratios (all *P*-values > 0.05).

Discussion

At the onset of senescence, sepal-removal plants of *Floerkea proserpinacoides* had less biomass, fewer flowers and fruits, and a lower standardized reproductive output than control plants, particularly at high light levels. These results indicate that sepals contribute significantly to plant carbon gain, and hence reduce costs associated with reproduction. However, sepal contribution was not more significant for the plant when light availability was reduced (for similar results see also: Jurik, 1985; Vu et al., 1985). Had it been the case, differences in performance would have been proportionally greater in shade than in full light. Yet, a larger photosynthetic surface would seem more advantageous for the plant at low rather than at high light







levels (Larcher, 2003). For instance, Salopek Sondi et al. (2000) demonstrated that green sepals of shaded plants of *Helleborus niger* L. (Ranunculaceae vs. Limnanthaceae) contributed more to the overall carbon budget than dark red sepals of full-light plants. In contrast, Heilmeier and Whale (1987) reported a lower contribution of the green floral bracts of *Arctium tomentosum* Mill. (Asteraceae vs. Limnanthaceae) to the carbon requirement of the flower heads in shaded versus full-light plants. They explained their results by an imbalance in shaded plants between the reduction in photosynthesis associated with lower irradiances and that in respiration associated with lower temperatures. A similar process might explain the results reported here for *F. proserpinacoides*.

Our results also indicate a limited ability of *F. proserpinacoides* plants, particularly those in full-light conditions, to adjust the photosynthetic capacity of their leaves to the carbon demands of reproduction. Thus, sepal-removal plants had a much lower standardized reproductive performance than control plants. This may suggest that leaf photosynthesis is not sink-driven. Indeed, in full-light conditions, control plants produced 38% more fruits per flower than sepal-removal plants, suggesting that when more carbon is available more fruits per flower are matured.

Nevertheless, sepal-removal decreased total biomass by 31% and 11% and fruit number by 53% and 30% at high and low irradiances, respectively. Bazzaz and Carlson (1979b) showed that reproductive structures of male and female inflorescences of *Ambrosia trifida* L., a monoecious species in Asteraceae (vs. Limnanthaceae), accounted for 41% and 51%, respectively, of the carbon required for reproduction in full-light conditions; our values for *F. proserpinacoides* are close to those estimated by these authors.

Flowering in *F. proserpinacoides*, as in other plant species, is not a costly process in comparison to fruit maturation (Stephenson, 1992; Hensel et al., 1994; Delesalle & Mooreside, 1995; Houle, 2002). One flower is produced at the base of each leaf, and thus flowering and growth cannot be dissociated (Cohen, 1971). Because sepals are photosynthetic and contribute to costs associated with

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Figure 2. Effects of light level and sepal removal on total number of flowers, carpels, and mature fruits of *Floerkea proserpinacoides* (Limnanthaceae). Mean + 1 s.e. (N = 12). *P*-values for randomized complete block design ANOVA.

Table 1. Effects of light level[1] and sepal removal on biomass ratios[2] (mean ± 1 s.e.) of *Floerkea proserpinacoides* (Limnanthaceae). See Materials and Methods for details.

Variable	Full light		Shade				
	Control	Sepal removal	Control	Sepal removal	P_L[3]	P_R	$P_{L\times R}$
Root ratio	0.025 ± 0.002	0.030 ± 0.002	0.030 ± 0.003	0.033 ± 0.005	0.2240	0.1321	0.6531
Stem ratio	0.357 ± 0.021	0.452 ± 0.020	0.412 ± 0.017	0.380 ± 0.020	0.7212	0.0280	0.0026
Leaf ratio	0.211 ± 0.015	0.258 ± 0.012	0.221 ± 0.015	0.285 ± 0.025	0.0882	0.0014	0.6391
Reproductive ratio	0.407 ± 0.032	0.260 ± 0.030	0.337 ± 0.021	0.302 ± 0.024	0.6092	0.0015	0.0366

[1] Full light: 202.3 μmol m^{-2} s^{-1} for a 7-week period; shade: 113.2 μmol m^{-2} s^{-1} for a 5-week period, then reduced to 59.2 μmol m^{-2} s^{-1} for an additional 2-week period.

[2] Root ratio: root mass/total biomass; stem ratio: stem and petiole mass/total biomass; leaf ratio: leaf mass/total biomass; reproductive ratio: reproductive mass/total biomass.

[3] P_L, P_R, $P_{L\times R}$: probability for the effects of light level and sepal removal and for their interaction, respectively. Randomized complete block design ANOVA.

reproduction, more of the carbon fixed by the leaves can be used to produce additional leaves and thus additional flowers, thereby optimizing reproduction. Fruit maturation, which occurs only at the end of the plant's life cycle, presumably uses up reserves previously accumulated in leaves, stems, and sepals (Bloom et al., 1985; Rose, 1991; Bazzaz & Ackerly, 1992; German et al., 2001; Houle, 2002). The carbon contribution of sepals to fruit maturation appears particularly significant for this plant, at least as much as does the temporal segregation of growth and fruit maturation (Ben Mokhtar & Houle, 2005). These traits allow *F. proserpinacoides* to successfully occupy a temporally ephemeral habitat while optimizing its reproductive output. Thus, they represent significant traits of the species' reproductive strategy.

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CONTENTS

Systematics and Evolution of *Ludwigia* Section *Dantia* (Onagraceae)
Ching-I Peng, Clifford L. Schmidt, Peter C. Hoch & Peter H. Raven 307

Revision of *Ancistrocladus* Wall. (Ancistrocladaceae) *Charlotte M. Taylor, Roy E. Gereau & Gretchen M. Walters* 360

Phylogeny, Morphological Evolution, and Speciation of Endemic Brassicaceae Genera in the Cape Flora of Southern Africa *Klaus Mummenhoff, Ihsan A. Al-Shehbaz, Freek T. Bakker, H. Peter Linder & Andreas Mühlhausen* 400

Congruence of a Phylogeny of Cordiaceae (Boraginales) Inferred from ITS1 Sequence Data with Morphology, Ecology, and Biogeography *Marc Gottschling, James S. Miller, Maximilian Weigend & Hartmut H. Hilger* 425

Photosynthate Contribution by Sepals Alleviates the Carbon Cost of Reproduction in the Spring Ephemeral *Floerkea proserpinacoides* (Limnanthaceae)
Ines Ben Mokhtar & Gilles Houle 438

Cover illustration. *Megacorax gracielanus* S. González & W. L. Wagner, first described as a new genus and species of the family Onagraceae from Mexico in *Novon* 12: 362, 2002. The generic name is based on the combination of the Greek words *mega*, large or great, and *korax*, raven, to honor Missouri Botanical Garden Director Peter H. Raven, author of numerous papers and monographs on many aspects of the family and one of our foremost advocates for conservation and sustainable use of the environment. The specific epithet honors Graciela Calderón Díaz-Barriga, major contributor to *Flora del Valle de México* and *Flora del Bajío* and mentor of several generations of students. The illustration is by Alice R. Tangerini (US).

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A REVIEW AND SURVEY OF BASICARPY, GEOCARPY, AND AMPHICARPY IN THE AFRICAN AND MADAGASCAN FLORA[1]

Nigel P. Barker[2]

ABSTRACT

A review of amphicarpy, basicarpy, and geocarpy is provided, and the definitions of these terms are clarified. Additional distinction is made between active and passive geocarpy. The literature on amphicarpy, basicarpy, and geocarpy is surveyed for reports of taxa displaying these traits, and a survey detailing basicarpy, amphicarpy, and geocarpy in the African and Madagascan flora is presented. Amphicarpy, basicarpy, or geocarpy is reported for 21 families and 40 genera of angiosperms. Interestingly, a number of holoparasites are basicarpic or geocarpic, but other than a predominance of species that occur in habitats with unstable substrates (arid or afroalpine), there appears to be little or no trend among the species listed that would enable the construction of a "profile" of features that would suggest that species or genera are predisposed toward being amphicarpic or geocarpic.

Key words: African flora, amphicarpy, basicarpy, geocarpy, seed dispersal.

Geocarpy was defined by van der Pijl (1982: 94) as "the burying near the mother plant of all diaspores . . .," a definition taken in turn from the work of Zohary (1962). As such, this mechanism results in seeds being dispersed short distances from the parent plant. While this may be construed as a method to ensure that the next generation have a suitable habitat in which to germinate, it also means that gene flow via the seed is extremely limited. This was considered by van der Pijl to be a

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[2]Molecular Ecology and Systematics Group, Department of Botany, Rhodes University, Grahamstown, 6140, South Africa. n.barker@ru.ac.za.

defensive strategy, and geocarpy was thus viewed as one of a number of mechanisms that result in atelechory, defined by van der Pijl (1982: 91) as "... the avoidance of too much of any dispersal and the inhibitory mechanisms for obtaining this."

There appears to be some confusion in the literature differentiating what van der Pijl (1982) referred to as full geocarpy (where flowers, and subsequently fruits, are formed underground) and a second type of geocarpy (where the flowers are borne above ground, but all the fruits subsequently develop below the soil surface). Note, however, that the definition of geocarpy given in the opening sentence relies on the fact that all fruits must develop underground, and thus the situations where plants bear both aerial and subterranean fruits are not covered by this definition. Instead, this latter strategy is generally referred to as amphicarpy (Cheplick, 1987, and references therein). Underground flowering is perhaps better referred to as geoflory and is rarely known, especially in the absence of the production of aerial flowers as well. Somewhat confusingly, Kaul et al. (2000: 40) used the term amphicarpic to refer to plants that bear fruits from flowers "which are *ab initio* underground" (with no mention of the co-existence of aboveground flowers), a different use of the term from van der Pijl (1982).

Amphicarpy was defined by Cheplick (1987) as plants in which at least some fruits are produced below the soil surface on specialized structures, in addition to aerial fruits on the same plant. This definition, if strictly applied, emphasizes where the seed is produced. As noted by Cheplick (1994: 119), the term amphicarpic really means "having two types of seed." Amphicarpic species sensu Cheplick thus produce aboveground and belowground (geoflorous) flowers. However, some species that have been considered amphicarpic bury some of their developing fruits following aerial flowering, a completely different process, but with the same result: subterranean and aerial seed set. Geocarpy may thus occur as a component of amphicarpy. Amphicarpic plants have only some of their seed underground, while other seeds develop and disperse in the normal fashion above ground. Amphicarpy appears to be usually found in plants from arid regions that occupy a niche that is ephemeral or susceptible to stochastic disturbances (Mandák, 1997, and references therein).

Amphicarpy is also often associated with cleistogamy (self-fertilization in an enclosed flower), especially of the basal or underground flowers, and heterodiaspory. The latter occurs as either or both heterocarpy (multiple forms of fruit) and heterospermy (multiple forms of seed, also termed seed heteromorphism by Imbert, 2002). To further complicate matters, seeds (either homospermic or heterospermic) from the same plant may be a mix of tachysporous (fast germinating) or bradysporous (slow germinating).

One of the more complex combinations of these strategies is found in the amphicarpic daisy *Catanache lutea* L. This species has both aerial and basal capitula. The aerial capitula are the "normal" daisy type, while the basal capitula are produced and flower above the soil surface, set seed, and are subsequently retracted 5–20 mm below the soil surface by contractile roots. Aerial capitula produce three different types of cypselae, and the subterranean capitula two kinds. The two different subterranean cypselae possess differing germination rates (De Clavijo, 1995). All these strategies provide a range of options for seeds derived from a single plant to survive and to reproduce in stochastic environments (van der Pijl, 1982). Mandák (1997) provided a detailed review of seed heteromorphism.

As might be apparent from the above, one problem encountered in researching this subject is that the terminology available appears to be used inconsistently. Some examples fail to draw the distinction between species that show both geoflory and subsequent geocarpy (full geocarpy sensu van der Pijl, which is almost always found in amphicarpic species) and species that have only aboveground flowers, but which, through specialization and growth of certain structures, bury the developing seed. Added to this distinction, the term basicarpy has been used for those plants that flower and fruit at ground level (van der Pijl, 1982). This term could, however, apply to all plants that are prostrate or trail along the ground, because it follows that all flowers will be produced at or close to ground level, rendering this definition somewhat irrelevant. While basicarpy is a meaningful term, it needs to be carefully defined to obviate the automatic inclusion of plants such as those that are prostrate. In an effort to clarify the confusion surrounding the use of various terms, a summary of these existing and newly created terms is presented in Table 1, and is explained (and used in subsequent examples) below.

I use the term basicarpy exclusively for those species that have flowers (including the ovary) at or slightly above ground level at all times during the flowering and fruiting cycle. I also use this term to further subdivide the variably applied term amphicarpy. As noted above, if the definition of amphicarpy is to be strictly applied, then geoflory

Table 1. Terminology to distinguish the different subtypes of amphicarpy and geocarpy.

Type	Subtype	Terminology
Subterranean fruiting from subterranean flowers		full geocarpy sensu van der Pijl (1982)
Subterranean fruiting from aboveground flowers	aboveground flowering, subsequent **burial by plant**	active geocarpy
	aboveground flowering, subsequent **burial by environment**	passive geocarpy
	aboveground flowering, with **ovary buried below ground,** often associated with underground storage organ	geophytic geocarpy
Fruiting at ground level		basicarpy
Two different floral and fruiting structures, one chasmogamous and aerial, the other often cleistogamous, usually at or below ground level	flowers and fruit produced **above ground level**	aerial amphicarpy
	flowers and fruit produced above and **below ground level**	amphi-geocarpy
	flowers and fruit produced above and **at ground level**	amphi-basicarpy

must occur. Amphicarpic species, at least as interpreted by some workers such as Stopp (1958), comprise plants with two kinds of flowers: aerial and basal (as opposed to subterranean). Often, the basal flower is cleistogamous. Clearly, this syndrome of aerial and basal flowers does not fit the definition of amphicarpy sensu Cheplick (1987). I thus refer to this kind of amphicarpy as amphi-basicarpy, in order to distinguish it from amphicarpy as defined by Cheplick (1987), which requires aerial and underground flowers and fruits. There is an additional variant of this, where the hidden (cleistogamous) flowers are not basal, but produced elsewhere on the plant. This is known to occur in some grasses, where cleistogamous flowers (cleistogenes) are hidden in the leaf sheaths associated with the aerial culms or aerial nodes (as opposed to a basal position). This form of seed production is known as cleistocarpy. This has been well studied in the aptly named grass *Amphicarpum purshii* Kunth (see Cheplick, 1994, for a summary). Other examples of grasses with this reproductive strategy include *Microlaena* R. Br. (notably *M. polynoda* Hook. f. and *M. stipoides* R. Br.; Connor & Matthews, 1977; Watson & Dallwitz, 1992), *Achnatherum* Beauv. (including the weedy *A. caudatum* (Trin.) S. W. L. Jacobs & J. Everett (Caro & Sanchez, 1971; Watson & Dallwitz, 1992), and some species of *Nassella* E. Desv. and *Stipa* L. (Watson & Dallwitz, 1992). I use the term aerial amphicarpy for this variant. Finally, the category of amphicarpic plants where aerial and subterranean fruits are produced, but where the subterranean fruits originate from aerial flowers, is termed here amphi-geocarpy.

The term geocarpy needs to be further refined, and I have subdivided this category, deliberately distinguishing between active, passive, and geophytic geocarpy, as some of the records of geocarpy given in this paper merit this distinction. In active geocarpy the plant physically responds in an active manner (by means of some form of growth or tropism, usually of the peduncle) to bury the seed. The classic example of this form of geocarpy is the peanut, *Arachis hypogaea* L., but Kaul et al. (2000) also cited *Trifolium subterraneum* L., *Vigna subterranea* (L.) Verdc. (= *Voandzeia subterranea* (L.) Thouars) and *Macrotyloma geocarpum* (Harms) Maréchal & Baudet (= *Kerstingiella geocarpa* Harms) as additional examples. Interestingly, all these taxa are of the family Leguminosae. In the Compositae, the amphicarpic *Catananche lutea* (discussed above) also shows active geocarpy in that the basal capitula are retracted underground after flowering. In contrast, I suggest the term passive geocarpy to include those species in which seeds are not dispersed from the parent but that are nonetheless buried while still attached to the parent plant. This burial is, however, not a result of the plant's actions, but of the actions of the environment: deposition of soil over the plant (or the infructescence) by the action of wind or water.

Another type of geocarpy is that in which the flower is produced above the ground, but the ovary and subsequent fruit remain below ground level at

all times. I propose the term geophytic geocarpy for plants that fit into this category, as many of the species that adopt this strategy are geophytes. This type of subterranean fruit retention is linked to the retention of the ovary underground, as described in several monocotyledons such as *Colchicum* L., *Crocus* L., and *Crinum* L. (Burtt, 1970). However, in the majority of the examples cited by Burtt, the fruits are subsequently elevated above the soil surface when ripe so as to ensure seed dispersal. The retention of the ovary underground might be a strategy to protect the developing seeds for as long as possible prior to their dispersal (Burtt, 1970). The geophytic geocarpy category as employed here is, however, not restricted to geophytes.

The Incidence of Amphicarpy and Geocarpy

This phenomenon is not widely reported, and the numbers of known amphicarpic and geocarpic species are low. Cheplick (1987) noted that amphicarpy was found in 26 species from nine plant families, and most frequently in the Leguminosae and Poaceae. Prior to this, Zohary (1937) reported approximately 30 species of amphicarpic plants, and this work highlighted the abundance of these species from Palestine, and their association with desert environments. Van der Pijl (1982) made reference to a number of taxa, but no clear number of amphicarpic or geocarpic taxa was offered. Kaul et al. (2000) cited 36 plant species that bear underground, cleistogamous flowers. Lev-Yadun (2000: 289) expanded this number to ". . . about 50 amphicarpic species and 20 geocarpic species . . ." The term amphicarpic as used in this latter paper refers to plants with both aerial and subterranean flowers, which is what I term amphi-geocarpic. In Israel, Lev-Yadun (2000) recorded eight amphicarpic species and eight geocarpic species out of a total flora of approximately 2500 species. The flora of Israel thus has a disproportionately high number of amphi- and geocarpic species, and this is attributed to the fact that these features are found more frequently in annual species (Kaul et al., 2000), and that the Israeli flora is rich in annuals (Shmida, 1981). Additional literature and internet searches have unearthed reports and observations of several additional taxa that are noted as either amphicarpic or geocarpic.

Active geocarpy (as defined here) has been reported in the Australian *Tribulopis* R. Br. (Zygophyllaceae) by Keighery (1982), the Nepalese and Himalayan *Lignariella hinkuensis* Kats. Arai, H. Ohba & Al-Shehbaz (Brassicaceae) by Al-Shehbaz et al. (2000), the Central Asian *Taphrospermum himalaicum* (Hook. f. & Thomson) Al-Shehbaz, Kats. Arai & H. Ohba (Brassicaceae) by Al-Shehbaz (2000) and *Euploca hypogaea* (Urb. & Ekman) Diane & Hilger (Heliotropaceae) by Diane et al. (in press). Kalin Arroyo (1981) listed *Astragalus* L., *Trigonella* L., *Trifolium* L., *Arachis* L. (mentioned above), *Tephrosia* Pers., and *Dolichos* L. as having species that are geocarpic.

In addition, Meney et al. (1990) reported an unusual form of amphicarpy in three species of the dioecious *Alexgeorgea* Carlquist (Restionaceae), where the female flowers are geoflorous and the male flowers aerial. *Halodule uninervis* (Forssk.) Asch. is a dioecious marine angiosperm seagrass that has geoflorous (and submerged) female flowers, and the fruits are released below the surface of marine sediments (Inglis, 2000). The family placement of this genus is confusing, as IPNI, TROPICOS, and the online Flora of North America variously place it in the Cymodoceaceae, Zosteraceae, Najadaceae, Hydrocharitaceae, and Potamogetonaceae. The first-mentioned family is the placement used for the *Flora of North America*.

Bruhl (1994) reported on amphicarpy in the Cyperaceae, citing examples of amphicarpic species in the genera *Schoenoplectus* (Rchb.) Palla and *Eleocharis* R. Br. The South African *Trianoptiles* Fenzl (comprising three species) is entirely amphicarpic (Bruhl, 1994; Haines & Lye, 1977). Note, however, that all these Cyperaceae taxa show what I termed here as amphi-basicarpy. Calviño and Galetto (2003) reported amphicarpy in *Cryptantha capituliflora* (Clos) Reiche, a high-altitude species of Boraginaceae from the Andes. The legumes have a number of amphicarpic genera; Kalin Arroyo (1981), citing Rivals (1953), reported amphicarpy from species of *Vicia* L., *Amphicarpa* S. Elliott ex Nuttall, *Vigna* Savi, and *Trifolium* L., and Tindale and Craven (1989) reported on amphicarpy in some species of *Glycine* Willd. In addition, web searches have revealed a number of other unpublished studies on amphicarpic species: *Centrosema rotundifolium* Mart. ex Benth., a South American legume (Müller et al., 2001), *Trifolium polymorphum* Poir. (Speroni & Izaguirre, 2003), and *Schoenoplectus hallii* (A. Gray) S. G. Sm. (Cyperaceae; Beatty et al., 2004). However, given the number of African species that my research has revealed as being amphicarpic, basicarpic, or geocarpic, there are probably many more taxa that can be added to this list, if they are adequately investigated.

Basicarpy, Amphicarpy, and Geocarpy in the African and Madagascan Flora

Literature surveys, web searches, and personal communications with a number of botanists result-

ed in a list of over 50 African or Madagascan taxa that are either amphicarpic, basicarpic, or geocarpic in some form. I have relied in particular on the works by Stopp (1958) and Agnew and Hedberg (1969) as starting points. It is quite possible that many more species have been noted as being amphicarpic or geocarpic, but the likely sources of such observations, notably flora treatments, are generally not available in electronic formats, and thus not searchable using modern computer-based methods. The recent exception to this is *Flora Zambeziaca,* launched in 2004, ⟨http://www.kew.org/efloras/search.do⟩, but this is not searchable for anything other than taxon names, a limitation that I hope will be addressed as technologies develop.

Agnew and Hedberg (1969: 215, 216) reported seven afroalpine species as being "strongly geocarpic," and listed a further twelve taxa that are "depositers" sensu Hylander (1929). Geocarpy in the afroalpine environment is considered by Agnew and Hedberg (1969) to be an adaptation to constant solifluction (the disturbance of the soil by the often daily cycle of freezing and thawing of soils at high altitudes). The considerable number of geocarpic taxa in both afroalpine and arid areas such as Israel (Lev-Yadun, 2000) is intriguing. Arid and afroalpine regions are two very different habitats, but both can comprise soils that are mobile. This makes seedling establishment difficult, and the burial of seeds may ensure reproductive success in such habitats.

I have only considered flowering plants in this list, but it must be noted that Stopp (1958) included some species of the aquatic fern genus *Marsilea* L., as well as a species of the lycophyte *Isoetes stellenbossiensis* A. V. Duthie. Table 2 lists angiosperm species that have either or both been observed or reported as geocarpic. The so-called "depositers" (sensu Agnew & Hedbeg, 1969), which simply release their seed at the base of the plant, have not been included in this list, as I feel that deposition is a general description that cannot readily be researched, and that deposition could be a prelude to further dispersal by means of specialist syndromes. Furthermore, some species that could be described as depositors may fit this description because they happen to be basicarpic. The distinction is thus difficult to make.

Each of the families represented in Table 2 are briefly discussed below, in alphabetical order. As noted by Cheplick (1987), confirming or verifying some of these reports is difficult, and I welcome communications from botanists who may have additional information or conflicting opinions.

APIACEAE

Agnew and Hedberg (1969) cited *Haplosciadium abyssinicum* Hochst., now known as *Trachydium abyssinicum* (Hochst.) Hiern, as an alpine geocarpic species. However, I have been unable to obtain any additional information on this species, and it is included here on the basis of this initial report.

ASTERACEAE

As noted above, fascinating examples of the diversity of amphicarpy may be found in members of this family, but examples of amphicarpy or geocarpy in African representatives of this family have not been well documented. Agnew and Hedberg (1969) reported geocarpy in *Haplocarpha rueppellii* (Sch. Bip.) Beauverd, and I have independently observed this in the field in the Bale Mountains, Ethiopia. While this species is obviously geocarpic, reflexing the short peduncle to force the capitulum onto the ground, another species in the genus, *Haplocarpha schimperi* (Benth. & Hook.) Beauverd, is even more strongly and obviously geocarpic. This species, known only from the Ethiopian and Eritrean highlands, has capitula borne on short peduncles. After flowering, these peduncles invert, forcing the capitulum with the developing cypselae into the soil (pers. obs.). Both species of *Haplocarpha* Less. prefer disturbed sites along streams and drainage lines, and both occur in the afroalpine zone, although *H. schimperi* is also quite widespread at lower altitudes, even being found in damp places in urban areas such as Addis Ababa (pers. obs.). Thus, although Agnew and Hedberg (1969) considered geocarpy to be an adaptation to solifluction of afroalpine soils, it appears that *H. schimperi* can successfully reproduce in areas that are not subject to solifluction, but that are, nonetheless, disturbed.

A third species of *Haplocarpha, H. nervosa* (Thunb.) P. Beauv., has also been observed both in the field and greenhouse as being actively geocarpic (see Fig. 1), and this can also be noted from herbarium specimens (e.g., *S. Schonland 3014, R. A. Dyer, 786,* both at GRA). This morphologically variable species is found in moist boggy habitats or along stream banks in montane regions of the Eastern Cape and Drakensberg of Kwa-Zulu Natal. *Haplocarpha nervosa* in the south, and *H. schimperi* and *H. rueppellii* in the north, may be examples of afromontane disjunct sister taxa.

Arctotheca populifolia (Bergius) Norl. is also listed in Table 2 as passively geocarpic. It inhabits sandy beaches of the southern and eastern coastline of Africa, and is one of the three main dune pio-

Table 2. African and Madagascan plants recorded as being amphicarpic or geocarpic. Where information is available, the nature of amphicarpy (as defined in Table 1) is described.

Family	Taxon	Form of reproduction	Distribution	Source
Apiaceae	*Trachydium abyssinicum* (Hochst.) Hiern	geocarpy (subtype unknown)	East Africa	Agnew & Hedberg (1969), as *Haplosciadium abyssinicum* Hochst.
Asteraceae	*Arctotheca populifolia* (Bergius) Norl.	passive geocarpy	Southern Africa	Barker (pers. obs.)
	Haplocarpha schimperi (Sch. Bip.) Beauverd	active geocarpy	African Mountain Chain, Ethiopia to Tanzania	Barker (pers. obs.); *Barker 1899* (ETH, GRA)
	Haplocarpha rueppellii Sch. Bip.) Beauverd	active geocarpy	African Mountain Chain, Ethiopia to Tanzania	Agnew & Hedberg (1969); *Barker 1906* (ETH)
	Haplocarpha nervosa (Thunb.) P. Beauv.	active geocarpy	South Africa, Zimbabwe	Barker (pers. obs.); *McKenzie 991* (GRA)
Balanophoraceae	*Mystropetalon polemannii* Harv.	basicarpy	Western Cape, South Africa	Kuijt (1969); Visser (1981)
	Mystropetalon thomii Harv.	basicarpy	Western Cape, South Africa	Kuijt (1969); Visser (1981)
	Sarcophyte sanguinea Sparrm.	basicarpy	South Africa	Kuijt (1969); Visser (1981)
Begoniaceae	*Begonia laporteifolia* Warb.	depositor (active geocarpy reported by van der Pijl, 1982)	Tropical Africa	van der Pijl (1982), as *B. hypogaea* Winkler; M. Sosef, (pers. comm.)
Commelinaceae	*Commelina benghalensis* L.	amphi-geocarpy	Central & East Africa, Madagascar	Stopp (1958); Cheplick (1987); Kaul et al. (2002)
	Commelina forsskalaei Vahl	amphi-geocarpy	Central & East Africa	Stopp (1958); Cheplick (1987)
Convolvulaceae	*Falkia repens* L.f.	active geocarpy	S and SW Cape, South Africa	van der Pijl (1982); Stopp (1958)
	Nephrophyllum abyssinicum A. Rich.	active geocarpy	Ethiopia and Eritrea	S. Edwards (pers. comm.)
Cucurbitaceae	*Cucumis humofructus* Stent	active geocarpy	Southern Africa	Stopp (1958)
	Kedrostis psammophila Bruyns	geophytic geocarpy	Southern Africa	Bruyns (1993)
Cyperaceae	*Bulbostylis humilis* Kunth	amphi-basicarpy	East Africa	Haines (1971)
	Bulbostylis glaberrima Kük.	amphi-basicarpy	East Africa	Haines (1971)
	Bulbostylis sp.	amphi-basicarpy	East Africa	Haines (1971)
	Scirpus lateriflorus J. F. Gmel.	amphi-basicarpy	East Africa	Haines (1971)
	Scirpus articulatus L.	amphi-basicarpy	East Africa	Haines (1971)
	Scirpus supinus L.	amphi-basicarpy	Southern Africa	Haines (1971)
	Scirpus praelongatus Poir.	amphi-basicarpy	East Africa	Haines (1971)
	Scirpus muricinux C. B. Clarke	amphi-basicarpy	East Africa	Haines (1971)
	Scirpus aberrans Cherm.	amphi-basicarpy	Madagascar	Haines (1971)
	Scirpus perrieri Cherm.	amphi-basicarpy	Madagascar	Haines (1971)
	Scirpus reductus Cherm.	amphi-basicarpy	Madagascar	Haines (1971)
	Trianoptiles solitaria (C. B. Clarke) Levyns	amphi-basicarpy	Western Cape, South Africa	Levyns (1943); Haines & Lye (1977)
	Trianoptiles capensis Harv.	amphi-basicarpy	Western Cape, South Africa	Levyns (1943); Haines & Lye (1977)
	Trianoptiles stipitata Levyns	amphi-basicarpy	Western Cape, South Africa	Levyns (1943)

Table 2. Continued.

Family	Taxon	Form of reproduction	Distribution	Source
Cytinaceae	*Cytinus capensis* Marloth	basicarpy	Western Cape, South Africa	Visser (1989)
	Cytinus sanguineus (Thunb.) Fourc.	basicarpy	Western Cape	Visser (1989)
	Cytinus sp.	basicarpy	Western Cape	Visser (1989)
Hydnoraceae	*Hydnora africana* Thunb.	geophytic geocarpy	Cape to Swaziland	Pole Evans (1926)
	Hydnora esculenta Jumelle & H. Perrier	geophytic geocarpy	Madagascar	Jumelle & Perrier (1912)
	Hydnora johannis Becc.	geophytic geocarpy	South Africa to Arabia	Musselman (1997), as *H. abyssinica*; Musselman & Visser (1987)
	Hydnora triceps Drege & E. Mey.	geophytic geocarpy	Namaqualand, South Africa	Visser (1989)
Hypoxidaceae	*Empodium* Salisb. (approx. 10 species)	basicarpy	Western, Central and Southern Africa	D. Snijman (pers. comm.); Hilliard & Burtt (1973)
	Pauridia longituba M. E. Thompson	geophytic geocarpy	Cape region, South Africa	G. Rowe (pers. comm.)
	Saniella occidentalis (Nel) B. L. Burtt	basicarpy	SW Cape, South Africa	J. Manning & D. Snijman (pers. comm.); Burtt (2000)
Iridaceae	*Babiana bainesii* Baker	geophytic geocarpy (possibly basicarpy)	Central South Africa	J. Manning (pers. comm.)
	Babiana hypogaea Burch.	geophytic geocarpy (possibly basicarpy)	Central South Africa	J. Manning (pers. comm.)
	Duthiastrum linifolium (Phill.) M. P. de Vos	geophytic geocarpy	Central South Africa	De Vos (1999a); J. Manning (pers. comm.)
	Ixia acaulis Goldblatt & J. C. Manning	geophytic geocarpy	Cape region, South Africa	De Vos (1999b); J. Manning (pers. comm.)
	Romulea stellata M. P. de Vos	geophytic geocarpy	Cape region, South Africa	J. Manning (pers. comm.)
	Syringodea bifurcata M. P. de Vos	geophytic geocarpy	Cape region, South Africa	Stopp (1958); De Vos (1983)
	Syringodea concolor (Baker) M. P. de Vos	geophytic geocarpy	Cape region, South Africa	Stopp (1958); De Vos (1983)
	Syringodea derustensis M. P. de Vos	geophytic geocarpy	Cape region, South Africa	Stopp (1958); De Vos (1983)
	Syringodea flanaganii Baker	geophytic geocarpy	Cape region, South Africa	Stopp (1958); De Vos (1983)
	Syringodea longituba (Klatt) Kuntze	geophytic geocarpy	Cape region, South Africa	Stopp (1958), as *S. leipoldtii*; De Vos (1983)
	Syringodea pulchella Hook. f.	geophytic geocarpy	Cape region, South Africa	Stopp (1958); De Vos (1983)
	Syringodea saxatilis M. P. de Vos	geophytic geocarpy	Cape region, South Africa	Stopp (1958); De Vos (1983)
	Syringodea unifolia Goldblatt	geophytic geocarpy	Cape region, South Africa	Stopp (1958); De Vos (1983)
Leguminosae	*Aeschynomene nematopoda* Harms	active geocarpy	East Africa	Stopp (1958); Gillett et al. (1971)
	Amphicarpaea africana (Hook.f.) Harms	amphi-geocarpy	Tropical Africa	B. Schrire (pers. comm.)
	Macrotyloma geocarpum (Harms) Maréchal & Baudet	active geocarpy	West and Central Africa	Hepper (1963), as *Kerstingiella geocarpa* Harms
	Tephrosia lupinifolia DC.	amphi-geocarpy	Tropical Africa	Cheplick (1987), Gillett et al. (1971)
	Trifolium subterraneum L.	active geocarpy	Cosmopolitan	Stopp (1958); B. Schrire (pers. comm.)
	Vicia amphicarpa Dorthes	amphi-geocarpy	Mediterranean North Africa	Plitmann (1973), as *Vicia sativa* subsp. *amphicarpa* (Dorth.) Ashers. & Graebn.

Table 2. Continued.

Family	Taxon	Form of reproduction	Distribution	Source
	Vigna subterranea (L.) Verdc.	active geocarpy	West and Central Africa	Hepper (1963), as *Voandzeia subterranea* (L.) Thouars
Moraceae	*Ficus sur* Forssk.	geocarpy (occasional)	Central-southern Africa	Van Noort (pers. comm.); http://www.figweb.org/ficus/subgenus_Sycomorus/section_Sycomorus/subsection_Sycomorus/Ficus_sur.htm
	Ficus trichoclada Baker	geocarpy	Madagascar	Van Noort (pers. comm.); http://www.figweb.org/ficus/subgenus_Sycomorus/section_Sycomorus/subsection_Sycomorus/Ficus_trichoclada.htm
	Ficus vogeliana (Miq.) Miq.	geocarpy	Tropical Africa	Van Noort (pers. comm.); http://www.figweb.org/ficus/subgenus_Sycomorus/section_Sycomorus/subsection_Sycomorus/Ficus_vogeliana.htm
Poaceae	*Enneapogon desvauxii* P. Beauv.	amphi-basicarpy	Namibia, Northern Cape of South Africa	Stopp (1958)
	Libyella cyrenaica Pamp.	amphi-geocarpy	Libya & Morocco	Watson & Dallwitz (1992)
Polygonaceae	*Emex australis* Steinh.	amphi-geocarpy	Cosmopolitan	Stopp (1958)
Primulaceae	*Anagallis kingaensis* Engl.	active geocarpy	Tropical Africa	Taylor (1958); Stopp (1958)
	Anagallis oligantha P. Taylor	active geocarpy	Tropical Africa	Taylor (1958); Stopp (1958)
Ranunculaceae	*Ranunculus cryptanthus* Milne-Redh. & Turrill	possible active geocarpy	East Africa	Milne-Redhead & Turrill (1952); Agnew & Hedberg (1969)
	Ranunculus oreophytus Delile	active geocarpy	East Africa	Milne-Redhead & Turrill (1952); Agnew & Hedberg (1969)
	Ranunculus stagnalis Hochst. ex A. Rich.	possible active geocarpy	East Africa	Milne-Redhead & Turrill (1952); Agnew Hedberg (1969)
Rubiaceae	*Galium ankaratrense* Puff	active geocarpy	Madagascar	Kiehn & Puff (1987)
Scrophulariaceae	*Limosella africana* Gluck	geocarpy (subtype unknown)	East Africa	Agnew & Hedberg (1969)
	Limosella capensis Thunb.	geocarpy (subtype unknown)	South Africa	Stopp (1958)
	Limosella macrantha R. E. Fr.	geocarpy (subtype unknown)	East Africa	Agnew & Hedberg (1969)
Urticaceae	*Laportea ovalifolia* (Schumach.) Chew	amphi-geocarpy	Tropical Africa	Engler (1895); Rendle (1917); Cheplick (1987), all as *Fleurya podocarpa* Wedd. var. *amphicarpa* Engl.; Friis (1991)

neers in this habitat. It has a rapid growth rate and forms small nabkha dunes (hummocks of wind-blown sand trapped by the leaves; Hesp & McLachlan, 2000). The capitula are held more or less erect and are obviously insect-pollinated. However, following anthesis, the capitulum closes and the peduncle relaxes such that it becomes procumbent. Subsequent burial by the accumulation of wind-blown sand occurs, and the seeds are either not released from the infructescence, or are only released if it is damaged by subterranean herbivores. The seeds are quite large, lack a well-developed pappus, and are woolly (McKenzie et al., 2005, this issue). This latter feature is possibly a water-retention mechanism, and these cypselae will germinate in situ, close to the parent plant (Knevel, 2002; Knevel et al., 2002).

Interestingly, these three species of *Haplocarpha* and *A. populifolia* are from the predominantly African subtribe Arctotidinae (tribe Arctotideae), and it is tempting to infer a close phylogenetic relationship of these species on the basis of this reproductive strategy. Results from preliminary molecular systematic studies (Funk et al., 2004; McKenzie et al., unpublished) suggest that *Haplocarpha* is highly polyphyletic, but relationships within this tribe are not yet fully resolved so this hypothesis awaits testing.

BALANOPHORACEAE

In southern Africa, *Sarcophyte sanguinea* Sparrm. parasitizes the roots of *Acacia* L. species. This species is dioecious and relies on flies for pollination, as the small flowers, produced at ground level, smell of carrion. This species, which I consider to be basicarpic, has compound fruits made up of the fused ovaries, which ripen into a fleshy mass. It is thought that these are animal-dispersed (Kuijt, 1969). *Mystropetalon* Harv. is a monoecious genus of two species from the southwestern Cape, South Africa, and produces spike-like inflorescences slightly above ground level. Male flowers are terminal to the female flowers on these spikes, and the inflorescences are protogynous. The seeds possess an elaiosome and are ant-dispersed (Kuijt, 1969; Visser, 1981). As these spikes are produced at ground level, these species are considered basicarpic.

BEGONIACEAE

Van der Pijl (1982) reported geocarpy in *Begonia hypogaea* Winkler (now known as *B. laporteifolia* Warb.), an occupant of African rain forests. This species grows near streams and produces a berry, but that is all that appears to be known about this species. However, M. Sosef (pers. comm.) considers this species to merely hold its fruits close to the ground, where they disintegrate, releasing the seeds in the vicinity of the parent. This species should thus be considered as a depositor sensu Agnew and Hedberg (1969), but is listed here owing to its previous categorization as geocarpic.

COMMELINACEAE

Kaul et al. (2000) cited five species in this family as having both cleistogamous underground flowers and aboveground flowers (amphi-geocarpy). As with many such species, the fruits from these two types of flowers are dimorphic. *Commelina benghalensis* L. is well studied in this regard (cf. Kaul et al., 2002).

CONVOLVULACEAE

Nephrophyllum abyssinicum A. Rich. is a member of the small tribe Dichondreae, the basal tribe in the family (Austin, 1997). It is an actively geocarpic species that is found in the highlands of Ethiopia and Eritrea, where it is recorded as occurring in heavily grazed pastures, open ground, and between crevices of rocks (Demissew & Austin, 1995). It is a prostrate herb, rooting at the nodes, with axillary flowers. The fruit is a utricle that develops underground from an elongating pedicel that pushes it below the soil surface. There are also reports of geocarpy within the closely related genus *Falkia* L. f., another member of the tribe Dichondreae, with species found in both Ethiopia and southern Africa. Van der Pijl (1982) included the southern African *Falkia repens* L. f. in his discussion of geocarpy, but omitted further details. This species was described by Stopp (1958, who cited it as *F. dichondroides* Baker) as a prostrate plant, in which the developing fruit is driven into the ground (also noted by Meeuse & Welman, 2000). In this species it was noted that the success of fruit burial was dependent on the substrate conditions. Stopp (1958) also considered *Dichondra* J. R. Forst. & G. Forst. to be similar in this regard, but provided no further discussion. Only the cosmopolitan *Dichondra micrantha* Urb. is known from Southern and East Africa (Verdourt, 1969; Austin, 1998; Meeuse & Welman, 2000), but none of these works makes any reference to fruit burial in this species. The seed development and dispersal of all members of the tribe Dichondreae are worthy of further investigation.

A
C

CUCURBITACEAE

Two geocarpic species are known from this family. Stopp (1958) included *Cucumis humofructus* Stent in his list of geocarpic taxa from southern Africa, as the plant actively buries the fruit of this species. However, as noted by van der Pijl (1982), the burial of fruit in this instance may not be a mechanism to ensure atelochory (lack of dispersal, also termed antitelochory by workers such as Ellner & Shmida, 1981) as the fruits are dispersed by aardvarks, which seek out the fruit as a source of water, and incidentally disperse the seeds far and wide following passage through the animal's gut (Meeuse, 1958). Thus this species is actively geocarpic, but the animal dispersal agent ensures that the seeds are widely dispersed, a situation that is probably unusual in geocarpic taxa.

Kedrostis psammophila Bruyns is found in Namaqualand, South Africa, and is usually prostrate, with separate male and female flowers. The female flowers develop from underground stems, and the ovary (and developing fruit) is retained below ground at all times, while the perianth is produced above ground (Bruyns, 1993). This species thus falls into the geophytic geocarpy category. The fruits are spherical, approximately 20 mm in diameter, and have 8 to 10 seeds. The fruits are possibly dispersed by moles, but this has not been observed or tested (Bruyns, 1993).

CYPERACEAE

There have been several reports of amphicarpy in the form of amphi-basicarpy in this family, which appears to have the greatest number of amphicarpic species in the African flora. Haines's (1971) report of amphicarpic taxa in East Africa probably only scratches the surface of the actual number of species in this family with this trait. A thorough investigation by cyperologists will probably find many more such taxa. In the cases noted in Table 2, the species possess aerial flowers as well as basal flowers protected by the leaf sheaths. The basal flowers usually produce larger seeds that may have a similar or different surface ornamentation (Haines, 1971). The unusual Cape genus *Trianoptiles* Fenzl has been studied quite extensively (Levyns, 1943; Haines & Lye, 1977; Bruhl, 1994). The comparatively large number of reports of amphicarpic species in this family might indicate that this strategy is an adaptation to ephemerally moist environments.

CYTINACEAE

This small family comprising the holoparasitic genera *Bdallophyton* Eichler and *Cytinus* L. was previously considered part of the Rafflesiaceae, but Nickrent et al. (2004) demonstrated that these two genera (as Cytinaceae) are related to the Malvales. There are three African and at least one Madagascan species of *Cytinus*, as well as species from the Mediterranean region (⟨http://www.science.siu.edu/parasitic-plants/Cytinaceae⟩). These species are either monoecious (the European *C. hypocistis* L.) or dioecious (*C. capensis* Marloth and *C. sanguineus* (Thunb.) Fourc.), and like the Hydnoraceae, they produce flowers from underground shoots and the fruits are borne at ground level. They are thus considered to be basicarpic. The fruits contain "several thousand" seeds (Visser, 1981: 63), which are thought to be dispersed when the fruit dries and cracks open, although Kuijt (1969) reported the presence of an elaiosome, suggesting ant dispersal.

HYDNORACEAE

This family of holoparasites is thought to be a Gondwanan relict. There are three species of *Hydnora* Thunb. in Africa and one in Madagascar, all of which live almost entirely below ground. The fruit has been described by Musselman (1997: 17) as ". . . a subterranean fleshy berry with a woody pericarp; seeds numerous in a flesh-coloured pulp, minute." The African species produce hermaphrodite flowers, while the Madagascan *H. esculenta* Jumelle & H. Perrier is monoecious. Flowers are predominantly subterranean, opening at the surface. In *H. triceps* Drege & E. Mey., the flowers open below ground, and pollinating insects (blowflies) enter through cracks in the soil (Visser, 1989). In *H. africana* Thunb. the flowers open above ground, and attract dermestid beetles. Following pollination the fruits mature below ground and are dispersed by jackals, porcupines, and baboons (Pole Evans, 1926). They are also eaten by humans (Musselman, 1997; Musselman & Visser, 1989). *Hydnora johan-*

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Figure 1. —A. *Haplocarpha nervosa*, showing capitulum on short peduncle, rosette growth form, and two reflexed peduncles of developing geocarpic infructescences at 9 and 7 o'clock. —B. Hirsute form of *H. nervosa* in the field, showing peduncle reflexing from the center of the rosette of leaves. —C. Details of reflexed peduncle and developing geocarpic infructescence. (A & C photographed in cultivation at Rhodes University from *McKenzie 991*, GRA.)

nis Becc. is the most widespread species, and its fleshy fruits are large (10–15 cm) and completely subterranean (Musselman & Venter, 1987). The fruits of the Madagascan species have been documented as having a juicy, white pulp, with a sour taste, being eaten by humans and lemurs (Jumelle & Perrier, 1912; ⟨http://bibliophile.mc.duke.edu/gww/Berenty/Plants/Hydnora-esculenta/index.html⟩). These species thus best fit the category of geophytic geocarpy, as the entire plant spends its life underground. For more on this intriguing group see ⟨http://www.odu.edu/webroot/instr/sci/plant.nsf/pages/hydnoraplant⟩ and ⟨http://www.science.siu.edu/parasitic-plants/Hydnoraceae⟩.

HYPOXIDACEAE

Considerable confusion arose during my investigations into this family. The Hypoxidaceae (and the Iridaceae) contain a number of species that have subterranean ovaries (Burtt, 1970), suggesting that these taxa would also be geocarpic. However, consultation with experts in these families has resulted in reports (published and unpublished observations) that suggest that the subterranean ovary may often become aerial as the fruit ripens and approaches dehiscence. *Saniella occidentalis* (Nel) B. L. Burtt possesses basal or subterranean ovaries, which are retained below ground when mature (Burtt, 2000). In contrast, the closely related *Empodium* Salisb. (a genus of 8 to 10 species) has a similar morphology (Hilliard & Burtt, 1973), but it is not clear if all species are basicarpic or geocarpic. D. Snijman (pers. comm.) reports that in *Saniella occidentalis*, *Empodium plicatum* Salisb., *E. namaquensis* (Baker) M. F. Thompson, and *E. flexile* M. F. Thompson ex Snijman, the mature fruit is pushed from the soil by an extension of the pedicel. This report for *Saniella* conflicts with Burtt's (2000) observations. Until clarity on the phenology of these species has been obtained, these taxa may be best considered as basicarpic, possibly even fitting with Agnew and Hedberg's (1969) depositor category. Similarly, *Rhodohypoxis rubella* Nel bears its fruit at or below ground level (basicarpic), while another (undescribed) species from marshy habitats is described as having fruit on an erect flower stalk that bends over to deposit the fruit on the ground (Hilliard & Burtt, 1973).

Pauridia longituba M. E. Thompson is a small geophyte that produces its flowers above ground while retaining the ovary underground throughout its life. These mature fruit capsules are thin-walled and indehiscent, fragmenting irregularly to release the seeds. A second species, *P. minuta* T. Durand & Schinz, produces the flower entirely above ground, but post-flowering the pedicel recurves and releases the seeds at the base of the parent plant (G. Rowe, pers. comm.). This species thus fits the category of a depositor sensu Agnew and Hedberg (1969).

IRIDACEAE

There are several taxa in this predominantly southern African geophyte family that have evolved flowers that retain the inferior ovary underground, and as noted above, Burtt (1970) reported this morphology for the European *Crocus* as well. In these taxa, the long, tubular perianth is exserted above ground, but developing fruits remain underground. The taxa in which this occurs are all from the subfamily Ixioideae, tribe Ixieae, suggesting that there may be a phylogenetic predisposition for this pattern of reproduction.

The genus *Syringodea* Hook. f. was first reported by Stopp (1958) as fitting what he considered to be the definition of basicarpy. The eight species in this genus all flower above ground, with the ovary retained underground, where it develops and is retained, and thus falls in my subtype of geophytic geocarpy. The fruit capsule in this genus is hygrochastic, and seed dispersal occurs when the capsule opens in damp or wet conditions, or when the capsule disintegrates with age. Burtt (1970) reiterated Stopp's (1958) reports that in *S. leipoldtii* (now known as *S. longituba* (Klatt) Kuntze) the upper part of the capsule emerges from the soil, where the hygrochastic valves split when wetted and some of the seeds are dispersed. The remaining seeds are retained and will germinate in situ.

Like species of *Syringodea*, *Duthiastrum linifolium* (Phill.) M. P. de Vos also possesses flowers with subterranean bases, and according to J. Manning (pers. comm.) the ovary and fruit remain buried. Similarly, *Ixia acaulis* Goldblatt & J. C. Manning has a buried ovary and is the only species in the genus with this feature. J. Manning (pers. comm.) also indicated that certain species of *Tritonia* Ker Gawl. and *Hesperantha* Ker Gawl. may also have this morphology, but details of these taxa have not been included here as no clear indication of the floral structure and the possible type of geocarpy could be found in the literature.

Two species of *Babiana* Ker Gawl. exhibit either geophytic geocarpy or basicarpy, the exact nature of the position of the mature fruit being unclear. This genus has several species that produce flowers at or near ground level, and in the instance of the two species listed in Table 2, J. Manning (pers.

comm.) observed the presence of an underground ovary (and developing fruit), which may be a mechanism to avoid seasonal temperature extremes, as it takes several months for the fruit to mature.

LEGUMINOSAE

Vigna subterranea (the bambara groundnut) and *Macrotyloma geocarpum* are actively geocarpic legumes from dry savanna areas of northern Cameroon and central Africa (Hepper, 1963; Kalin Arroyo, 1981; van der Pijl, 1982). Both these species produce aerial flowers but bury the developing fruit. When first discovered, these species were under limited cultivation as a food source for humans (Hepper, 1963). Subsequently, *V. subterranea* has become an important crop in many countries of tropical Africa (Linnemann, 1993; Pasquet et al., 1999), but *M. geocarpum* is disappearing from traditional food production (Pasquet et al., 2002).

From southern Africa, Stopp (1958) reported *Trifolium subterraneum* L. as being geocarpic. This species originates from the Mediterranean region, and Stopp (1958) considered it to be a neophyte in the Cape region. Indeed, internet searches suggest that this species is of agricultural value, and is cosmopolitan, but it is also listed as a weed by the Global Compendium of Weeds (⟨http://www.hear.org/gcw/html/index.html⟩). Few additional details are provided by Stopp (1958) who noted that the fruits are shallowly buried, but internet resources (such as ⟨http://www.fao.org/ag/AGP/AGPC/doc/Gbase/DATA/pf000351.HTM⟩) imply that the fruits are actively buried.

Aeschynomene nematopoda Harms is a scandent or trailing herb and is considered here to be actively geocarpic. This was first recorded by Stopp (1958), who provided a quotation from Harms, comparing this plant to the peanut, *Arachis hypogaea*. Gillett et al. (1971) noted in the *Flora of Tropical East Africa* that the pods develop below the ground, and suggested that herbarium specimens lack fruits because they break off when the plant is removed from the soil.

Vicia amphicarpa Dorthes from the Mediterranean region of North Africa is amphicarpic (according to Plitmann, 1973, as *Vicia sativa* subsp. *amphicarpa* (Dorthes) Ashers. & Graebn.), and this species is considered here to be amphi-geocarpic. *Tephrosia lupinifolia* DC. has been reported by Stopp (1958) as amphicarpic and is annual and inhabits sandy regions. Gillett et al. (1971: 167–169) illustrated and described this species as having normal inflorescences as well as occasionally producing axillary pseudoracemes near the base of the stem. These push underground when growing in sandy soil and bear small cleistogamous flowers. The subterranean pods are indehiscent and usually contain a single seed or sometimes two. This species is thus amphi-geocarpic.

Amphicarpaea africana (Hook. f.) Harms is the only African species of this small genus. The American species *A. bracteata* (L.) Fern is known as the "Hog Peanut." It appears that this genus is also amphi-geocarpic, but interestingly, Gillett et al. (1971) made no mention of amphi-geocarpy in their description of *A. africana* in the *Flora of Tropical East Africa*.

MORACEAE

The genus *Ficus* L. is large, and van der Pijl (1982) noted that some (unlisted) species are geocarpic. Some species of *Ficus* sect. *Sycomorus* bear syconia at or just below ground level on branchlets produced from the trunk and lower branches. In some species (listed in Table 2) these can become geocarpic. Other species such as *F. mauritiana* Lam., *F. tiliifolia* Baker, *F. polyphlebia* Baker, and *F. botryoides* Baker may also be potentially geocarpic in this manner, but this is not the usual form of fruiting (S. van Noort, pers. comm.), and the inclusion of this genus in a list of amphicarpic or geocarpic taxa is thus tentative. Given the attractive nature of the fruit, and the long life span of the species, it is unlikely that this is a strategy to retain seeds in the same location as the parent, but rather to make them accessible to dispersal agents.

POACEAE

Cleistogamy is well known in the grasses (see Campbell et al., 1983; Connor, 1987, for reviews) and usually occurs as a variant of amphicarpy (I list several examples of aerial amphicarpic grasses above). Campbell et al. (1983) indicated that eight species of cleistogamous grasses are known from Africa, but these are not named. I have not been able to find records of that many taxa. It is important to note that cleistogamy does not equate to geocarpy and that only two genera of grasses show underground cleistogamy (i.e., are geoflorous). Campbell et al. (1983) used Dobrenz and Beetle's (1966) term rhizanthogene for the underground flowers borne on specialized rhizomes, and indicated that there are eight species from four genera that possess these.

Connor (1979) reported several grass species that have cleistogenes—flowers at ground level enclosed by leaf sheaths. This is the same syndrome as reported in the Cyperaceae (above) and may be

considered as a borderline case of geocarpy: that termed basicarpy by van der Pijl (1982) and amphibasicarpy here. This syndrome appears predominantly in New World grasses, and the majority of the examples of aerial amphicarpy cited above are taxa of the subfamily Pooideae. However, it is also known from tribe Pappophoreae (subfamily Chloridoideae), an Old World group, a southern African example being *Enneapogon desvauxii* P. Beauv., an amphi-basicarpic annual species found in the arid western parts of southern Africa (Stopp, 1958, as the synonym *E. brachystachyus* Stapf). In this species, as is the general trend in amphicarpic grasses, the basal flowers produce a seed that is considerably larger than those from the aerial flowers. This larger seed is not readily released, as the disintegration of the leaf sheath is required to liberate it. Amphi-geocarpy is also found in *Libyella cyrenaica* Pamp., a monotypic genus of subfamily Pooideae. This plant, described by Clayton and Renvoize (1986) as a minute annual, grows in coastal sands and possesses hidden cleistogenes in the leaf sheaths as well as underground (Watson & Dallwitz, 1992).

POLYGONACEAE

Stopp (1958) cited *Emex australis* Steinh., a weed of South African origin, as possessing aerial and subterranean fruit. Surprisingly, given its declared weed status in several countries, I could find no mention of this seed heteromorphism on any weed-related web site I visited. Its sister species, *Emex spinosa* (L.) Campd., has also been documented as amphi-geocarpic, having both aerial and subterranean seeds (Evenari et al., 1977). In this species, the geocarpic seeds are approximately four times the size of the aerial seed and have different germination requirements (Weiss, 1980). It is thus possible that *E. australis* has a similar amphi-geocarpic nature.

PRIMULACEAE

In a postscript, Stopp (1958) cited Taylor's (1958) work on tropical African Primulaceae in which the actively geocarpic nature of *Anagallis kingaensis* Engl. is first described. Stopp (1958) stated that this is the first record of geocarpy in the family, but that there are some basicarpic species in *Anagallis* L. as well as *Cyclamen* L. and *Lysimachia* L. Taylor (1958) noted that in *A. kingaensis*, the pedicel elongates, reflexes, and becomes buried as the fruits ripen. Taylor (1958) noted that *A. oligantha* P. Taylor is closely related to *A. kingaensis* and made no mention of geocarpy in this species, but Stopp (1958) considered it to be geocarpic.

RANUNCULACEAE

Agnew and Hedberg (1969) listed three geocarpic species of *Ranunculus* L. (Table 2). However, of these three species, only *R. oreophytus* Delile is clearly described by Milne-Redhead and Turrill (1952) as being actively geocarpic. In this species, curvature of the pedicels buries the spherical heads in the soil. The remaining two species listed in Table 2 are described merely as having achenes in spherical heads on reflexed pedicels, a behavior they have in common with *R. oreophytus*, so it is possible that these two species are also actively geocarpic.

RUBIACEAE

Geocarpy has been reported in the Madagascan *Galium ankaratrense* Puff by Kiehn and Puff (1987). This species is found at high altitudes in the Ankaratra mountains. It is cushion-forming and grows in moist, sheltered places. After flowering, the pedicels elongate up to 40 mm in length, pushing the developing fruits into the ground. The seeds germinate under the mother plants, further adding to the dense cushion growth form (Kiehn & Puff, 1987).

SCROPHULARIACEAE

Two species of *Limosella* L. noted in Table 2 are afroalpine species recorded by Agnew and Hedberg (1969) as being geocarpic. The third species, *L. capensis*, is listed as geocarpic by Stopp (1958). *Limosella* comprises small aquatic plants, commonly known as mudworts. Some species of the genus have widespread distributions, thought to be mediated by bird dispersal of the small seeds that stick together along with mud to birds' legs (Kornhall, 2004). To the best of my knowledge, this dispersal explanation has not been tested, but I have observed the fruit of one of the southern African taxa being produced both on the surface and beneath the mud of shallow temporary water bodies (voucher *Barker 1922*, GRA). An accurate identification of this specimen to species level is not possible, and Hilliard and Burtt (1986) noted that a taxonomic revision of the African species is needed. The presence of geocarpy in other species of *Limosella* needs to be investigated.

URTICACEAE

Little is known about *Fleurya podocarpa* var. *amphicarpa*, the amphicarpic status of which was first

noted by Engler (1895) and again cited by Cheplick (1987). This taxon is now known as *Laportea ovalifolia* (Schumach.) Chew, and Friis (1991: 89) in *Flora Zambesiaca* merely noted that "geocarpic fruits may occur," while earlier, Rendle (1917) noted that one specimen comprised fruits that seemed to have been buried. These reports suggest that this species may be amphi-geocarpic.

Can Amphicarpic and Geocarpic Species Be Characterized?

Cheplick (1994) listed four adaptive advantages of amphi-geocarpy. These are the retention of offspring in suitable microhabitats (the mother site theory sensu Zohary, 1937, 1962), and the protection of seeds from microenvironmental extremes, fire, and herbivores or predators. Underground fruits may thus be important in maintaining the population in situ, unless they have specific adaptations for animal dispersal as noted, for example, in *Hydnora* and *Cucumis* discussed above. Assuming a lack of dispersal, the consequences of antitelochoric subterranean seed production include the lack of genetic exchange between the cleistogamous flowers leading to inbreeding depression, the high energy costs associated with the production of larger underground reproductive structures, limited dispersal, sibling competition among offspring, and exposure to underground herbivores and seed predators (Cheplick, 1994). For species that are exclusively geocarpic, these consequences (notably the genetic ones) would be further exacerbated by the lack of xenogamy. In light of these trade-offs, it might be expected that an amphicarpic or geocarpic strategy would only evolve under certain environmental conditions: conditions that, if known, could be used to predict the presence of amphicarpy, basicarpy, or geocarpy.

While the known amphicarpic and geocarpic taxa listed here are restricted to one continent (Africa, including Madagascar), this list has added to our knowledge of this unusual form of reproductive biology. The limited numbers of species make it difficult to draw any meaningful correlations with habit or habitat that would support any predictions. However, as noted above, species that bury their seeds usually have flowers or inflorescences at or near ground level. Thus species that are prostrate, scandent, cushion-forming, or rosette-forming may be candidates for geocarpy, and should be carefully investigated for it. From my investigations, it is apparent that some observations of geocarpy have been accidental and depend on good field observations and thorough plant-collecting techniques. Similarly, observations of amphi-basicarpy in caespitose taxa such as sedges and grasses require careful dissection of basal leaf and sheathing structures to locate these well-hidden fruits and seeds. Even herbaceous taxa that bear inflorescences from basal or ground-level branches should be treated with suspicion, and carefully examined and collected. Those geophytic taxa with ovaries held at or below ground level are obviously candidates for the geophytic geocarpy category, but careful observation of flower and fruiting phenology is required in order to rule out active geocarpy.

The species in Table 2 are often found in either arid areas where the substrate can be unstable, or high-altitude afroalpine regions in damp to wet habitats, also with potentially unstable soils. Thus the hypothesis of a link between geocarpy and life on unstable substrates, in either arid environments (as noted by Zohary, 1962) or afroalpine soils subject to erosion or solifluction (noted by Agnew & Hedberg, 1969) may have some merit. Ellner and Shmida (1981) noted that basicarpy is common in desert plants, and is often found in annual species that have hygrochastic diaspores. Several taxa listed here are found in arid regions, and some (notably the legumes) appear to occupy regions of low and strongly seasonal rainfall. Some of the Cyperaceae (e.g., *Trianoptiles*) occupy ephemerally wet habitats, as do the examples of *Rhodohypoxis* and *Limosella* noted here. The species of *Haplocarpha* (Compositae) occupy damp to wet disturbed sites, often along stream banks, which would be prone to flooding and associated erosion. Burial of seeds to avoid dispersal by runoff and associated erosion in this environment would be advantageous, an aspect also discussed in the context of flash floods in arid regions by Ellner and Shmida (1981).

As intimated by Cheplick (1994), basicarpy and geocarpy could limit seed-mediated gene flow, leading to increased isolation of populations, possibly resulting in increased speciation rates. Conversely, reduced gene flow between populations may result in genetic drift, fixation of alleles, and inbreeding depression, which could ultimately lead to local population (and possibly species) extinctions. Given this unusual reproductive strategy, it is surprising that no population genetic studies on geocarpic species (or comparing geocarpic and non-geocarpic congeners) have been carried out.

An additional reproductive phenomenon appears to be associated with some of the taxa in Table 2: that of floral dimorphism and various forms of monoecy. Species of *Ficus* (Moraceae) usually have male and female flowers within a single syconium, and in *Haplocarpha* (Compositae) the ray florets are

female, while disk florets are hermaphrodite, but this system is not uncommon in the family. Several of the holoparasitic species in *Kedrostris* (Cucurbitaceae), *Laportea* (Urticaceae), and *Emex* (Polygonaceae) are also monoecious. However, the species listed here have not been researched exhaustively, so the co-occurrence of amphicarpy, basicarpy, and geocarpy with monoecy could be coincidental.

In summary, amphicarpy, basicarpy, and geocarpy in all of their forms occur across a diverse range of flowering plants, edaphic and climatic conditions, and continents. In the context of the size of the flora of Africa and Madagascar, correlating the small number of amphicarpic, basicarpic, and geocarpic species listed here to environmental parameters provides very limited predictive power, but an association with unstable substrates appears to be a fairly common theme, and this biological enigma deserves further study.

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REVISIÓN SISTEMÁTICA DEL SUBGÉNERO *HARPOSTACHYS* DE *PASPALUM* (POACEAE: PANICOIDEAE: PANICEAE)[1]

Silvia Suyai Denham[2]

Resumen

En el presente trabajo se realiza una revisión sistemática del subgénero *Harpostachys* de *Paspalum*. Diversos autores han relacionado a las especies del grupo informal Decumbentes de *Paspalum* con el género *Thrasya* sobre la base de caracteres morfológicos, tales como la presencia de inflorescencias terminales y axilares en la última vaina foliar, racimos solitarios, presencia de gluma inferior y presencia de flor inferior estaminada. A través de un análisis filogenético usando caracteres morfológicos y anatómicos, Denham y Zuloaga concluyen que las especies del grupo Decumbentes y las especies del género *Thrasya* constituyen un grupo monofilético; éstos resultados son congruentes con estudios previos de filogenia molecular en la subfamilia Panicoideae. En el presente estudio 22 especies de *Thrasya* son transferidas al género *Paspalum*; se proponen 6 nombres nuevos para especies y 15 combinaciones nuevas: *Paspalum achlysophilum* (Soderstr.) S. Denham, *Paspalum auricomum* (A. G. Burm.) S. Denham, *Paspalum campylostachyum* (Hack.) S. Denham, *Paspalum carajasense* S. Denham, *Paspalum crucense* (Killeen) S. Denham, *Paspalum cultratum* (Trin.) S. Denham, *Paspalum calliferum* S. Denham, *Paspalum foliiforme* S. Denham, *Paspalum glaziovii* (A. G. Burm.) S. Denham, *Paspalum graniticum* (A. G. Burm.) S. Denham, *Paspalum huberi* S. Denham, *Paspalum mosquitiense* (Davidse & A. G. Burm.) S. Denham, *Paspalum oreophilum* (A. G. Burm.) S. Denham, *Paspalum orinocense* S. Denham, *Paspalum parvulum* (A. G. Burm.) S. Denham, *Paspalum procerum* S. Denham, *Paspalum schumannii* (Pilg.) S. Denham, *Paspalum seminudum* (A. G. Burm.) S. Denham, *Paspalum setosum* (Swallen) S. Denham, *Paspalum thrasyoides* (Trin.) S. Denham y *Paspalum trinitense* (Mez) S. Denham. Se establece el subgénero *Harpostachys* de *Paspalum* para incluir a las especies previamente tratadas en el grupo informal Decumbentes y en el género *Thrasya*. *Paspalum* subgénero *Harpostachys* incluye 39 especies que se distribuyen en los trópicos y subtrópicos de América, desde Estados Unidos de América hasta Argentina y Uruguay. Se incluye una clave para los subgéneros de *Paspalum*. Se definen los caracteres morfológicos y anatómicos del subgénero *Harpostachys*, se determina la distribución geográfica de las especies y se incluye una clave para su identificación. Se ofrecen descripciones, sinónimos actualizados, ilustraciones, fotografías y mapas de distribución de las especies aceptadas en el subgénero. Se transfieren a la sinonimia cinco taxas: *Paspalum culiacanum* Vasey [= *Paspalum adoperiens* (E. Fourn.) Chase], *Paspalum langei* (E. Fourn.) Nash, *Paspalum palmeri* Chase [= *Paspalum botterii* (E. Fourn.) Chase], *Thrasya reticulata* Swallen [= *Paspalum cinerascens* (Döll) A. G. Burm. & C. N. Bastos] y *Thrasya petrosa* (Trin.) Chase var. *ciliata* A. G. Burm. [= *Paspalum foliiforme* S. Denham]. Finalmente, se amplía la distribución geográfica de *P. cinerascens*, *P. subfalcatum*, *P. inconstans*, *P. calliferum*, *P. huberi*, *P. glaziovii* y *P. thrasyoides*.

Abstract

A systematic revision of *Paspalum* subg. *Harpostachys* is presented. Different authors have related species of the informal Decumbentes species group of *Paspalum* to genus *Thrasya*, on the basis of these morphological characters: the presence of terminal and axillary inflorescences in the upper foliar sheaths, solitary racemes, the presence of lower glumes, and a staminate lower flower. Through a recent phylogenetic analysis using morphological and anatomical characters, Denham and Zuloaga concluded that the species of the Decumbentes group and the species of genus *Thrasya* constitute a monophyletic group; this result is in agreement with previous molecular phylogenetic studies in the subfamily Panicoideae. In this study, the 22 species of *Thrasya* are transferred to *Paspalum*; six new species names and 15 new combinations are proposed: *Paspalum achlysophilum* (Soderstr.) S. Denham, *Paspalum auricomum* (A. G. Burm.) S. Denham, *Paspalum campylostachyum* (Hack.) S. Denham, *Paspalum carajasense* S. Denham, *Paspalum crucense* (Killeen) S. Denham, *Paspalum cultratum* (Trin.) S. Denham, *Paspalum calliferum* S. Denham, *Paspalum foliiforme* S. Denham, *Paspalum glaziovii* (A. G. Burm.) S. Denham, *Paspalum graniticum* (A. G. Burm.) S. Denham, *Paspalum huberi* S. Denham, *Paspalum mosquitiense* (Davidse & A. G. Burm.) S. Denham, *Paspalum oreophilum* (A. G. Burm.) S. Denham, *Paspalum orinocense* S. Denham, *Paspalum parvulum* (A. G. Burm.) S. Denham, *Paspalum procerum* S. Denham, *Paspalum schumannii* (Pilg.) S. Denham, *Paspalum seminudum* (A. G. Burm.) S. Denham, *Paspalum setosum* (Swallen) S. Denham, *Paspalum thrasyoides* (Trin.) S. Denham, and *Paspalum trinitense* (Mez) S. Denham. *Paspalum*

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[2]Instituto de Botánica Darwinion, Labardén 200, Casilla de Correo 22, San Isidro B1642HYD, Argentina. sdenham@darwin.edu.ar.

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subg. *Harpostachys* is established to include the species previously treated in the informal Decumbentes group and in *Thrasya*. *Paspalum* subg. *Harpostachys* comprises 39 species that are found in the American tropics and subtropics, from the United States to Argentina and Uruguay. A key to the subgenera of *Paspalum* is given. The morphological and anatomical characters of subgenus *Harpostachys* are defined, the geographic distribution of the species is determined, and a key to differentiate the species is included. Descriptions, updated synonymy, figures, photographs, and distribution maps are provided here. Five taxa are newly synonymized: *Paspalum culiacanum* Vasey [= *Paspalum adoperiens* (E. Fourn.) Chase], *Paspalum langei* (E. Fourn.) Nash, *Paspalum palmeri* Chase [= *Paspalum botterii* (E. Fourn.) Chase], *Thrasya reticulata* Swallen [= *Paspalum cinerascens* (Döll) A. G. Burm. & C. N. Bastos], and *Thrasya petrosa* (Trin.) Chase var. *ciliata* A. G. Burm. [= *Paspalum foliiforme* S. Denham]. Finally, the geographical distribution of *P. cinerascens*, *P. subfalcatum*, *P. inconstans*, *P. calliferum*, *P. huberi*, *P. glaziovii*, and *P. thrasyoides* is extended.
Key words: Decumbentes group, *Paspalum*, subgenus *Harpostachys*, *Thrasya*.

Paspalum L. pertenece a la tribu Paniceae de la subfamilia Panicoideae; comprende aproximadamente 330 especies (Zuloaga & Morrone, 2005) y se halla ampliamente distribuido, siendo frecuente en regiones tropicales, subtropicales y templado-cálidas de ambos hemisferios, con unos pocos representantes en el Viejo Mundo. Este género se caracteriza por sus inflorescencias racemosas, unilaterales, con espiguillas solitarias o en pares, gluma inferior comúnmente ausente, gluma superior y lemma inferior herbáceas a membranáceas y antecio superior endurecido. Desde el punto de vista fisiológico son plantas C_4, del subtipo NADP-ME y su anatomía corresponde al tipo MS (Hattersley & Watson, 1976; Brown, 1977); la mayor parte de las especies del género poseen un número cromosómico básico $x = 10$ y presentan reproducción sexual y apomíctica.

Debido al alto número de especies y a la amplia variación morfológica de las mismas, el género ha sido dividido en subgéneros, secciones o grupos informales principalmente sobre la base de caracteres morfológicos de la inflorescencia y de la espiguilla (Nees, 1829; Doell, 1877; Pilger, 1929, 1940; Chase, 1927, 1929; Clayton & Renvoize, 1986; Morrone et al., 1995, 1996, 2000, 2004; Cialdella et al., 1995; Denham et al., 2002; Zuloaga et al., 2004; Zuloaga & Morrone, 2005); sin embargo, no existe un esquema natural de clasificación para el género. Zuloaga y Morrone (2005) reconocen 3 subgéneros en *Paspalum*: *Anachyris* Chase, *Ceresia* (Pers.) Rchb. y *Paspalum*; estos autores indican que en el subgénero *Paspalum* aún no se encuentran caracteres diferenciales sólidos para establecer categorías infragenéricas, y sus especies se reúnen en grupos informales (Chase, 1929).

El grupo informal Decumbentes (Chase, 1929) del subgénero *Paspalum* se caracteriza por presentar inflorescencias terminales y axilares en la última vaina foliar, racimos usualmente solitarios, espiguillas pareadas, la gluma inferior presente, con un desarrollo desigual en las espiguillas superior e inferior de un par, siendo de mayor desarrollo en la inferior, y la pálea y flor inferior usualmente presentes.

El grupo Decumbentes comprende especies que fueron inicialmente tratadas bajo el género *Panicum* por presentar espiguillas con la gluma inferior desarrollada. Así, Trinius (1834) considera 12 secciones bajo el género *Panicum*, entre ellas sección *Harpostachys* Trin., en la que reúne especies con racimos solitarios, raro dos subconjugados y con espiguillas subsésiles, imbricadas, dispuestas en 1 a 2 o 4 series, en ocasiones subdísticas; este autor incluye en *Harpostachys* especies actualmente tratadas en el grupo Decumbentes de *Paspalum*, en *Thrasya*, en *Thrasyopsis* y en *Mesosetum*. Bentham (1881) y Bentham y Hooker (1883) consideran a las secciones *Harpostachys* y *Thrasya* (Kunth) Bentham en *Panicum*. Luego, Hackel (1901) considera a sección *Harpostachys* con categoría de subgénero en *Panicum* y hace una referencia directa a Hackel (1897), donde a su vez, cita a Bentham (1881).

Fournier (1875) establece el género *Dimorphostachys* para incluir especies en las que la gluma inferior está presente en la espiguilla inferior del par y está ausente en la espiguilla superior. Posteriormente, Fournier (1886) describe varias de las especies aquí tratadas bajo este género [*D. adoperiens* E. Fourn., *D. botterii* E. Fourn., *D. drummondii* E. Fourn., *D. ghiesbreghtii* E. Fourn., *D. langei* E. Fourn., *D. paspaloides* E. Fourn., *D. pedunculata* (Poir.) E. Fourn., *D. pilosa* (Lam.) E. Fourn., *D. schaffnerii* E. Fourn., *D. schaffnerii* var. *remotispicula* E. Fourn. y *D. variabilis* E. Fourn.]. Luego, Nash (1912) incluye las especies del género *Dimorphostachys* bajo *Paspalum*. Asimismo, Chase (1929) trata a *Dimorphostachys* bajo la sinonimia del género *Paspalum*, y a sus especies dentro del grupo informal Decumbentes.

Posteriormente, los estudios taxonómicos en el grupo Decumbentes han sido fragmentarios y sus especies han sido tratadas parcialmente en estudios florísticos o regionales: Pohl (1980), Judziewicz (1990), Tovar (1993), Pohl y Davidse (1994), Renvoize (1998), entre otros.

El género *Thrasya* fue establecido por Kunth (1815 [1816]) sobre la base de *Thrasya paspaloides* Kunth. Luego, Burman (1985 [1987]) realiza una completa revisión taxonómica del género. Diferentes autores han relacionado a las especies del género *Thrasya* con el grupo Decumbentes de *Paspalum* sobre la base de caracteres morfológicos (Chase, 1911; Burman, 1983, 1985 [1987]; Davidse, 1987; Burman & Bastos, 1988).

Estudios recientes de filogenia molecular en la subfamilia Panicoideae (Giussani et al., 2001), en la tribu Paniceae (Duvall et al., 2001) y en el género *Panicum* (Aliscioni et al., 2003), sugieren que *Paspalum* constituye un grupo parafilético por incluir a las especies de *Thrasya*. Denham y Zuloaga (en prensa) estudian las relaciones filogenéticas entre las especies del grupo Decumbentes y las especies de *Thrasya* a través de un análisis cladístico usando caracteres morfológicos y anatómicos, y obtienen resultados congruentes con los estudios de filogenia molecular. Estos autores concluyen que las especies del género *Thrasya* tienen un origen común con las especies del género *Paspalum* y que constituyen un grupo monofilético con las siguientes sinapomorfías: presencia de pedúnculos axilares en la última vaina foliar, gluma superior ligeramente menor a la espiguilla, márgenes de la lemma inferior doblados sobre el antecio superior y ausencia de papilas simples en el antecio superior.

Siguiendo el criterio de Denham y Zuloaga (en prensa), en el presente tratamiento se transfieren las especies de *Thrasya* al género *Paspalum*. Se establece formalmente el subgénero *Harpostachys* (Trin.) S. Denham de *Paspalum* para incluir a las especies previamente tratadas en el grupo informal Decumbentes y en *Thrasya*. Se estudia la morfología, anatomía y distribución geográfica de las especies; se describen los taxones previamente tratados en el grupo Decumbentes y se realiza una sinopsis de las especies anteriormente tratadas en el género *Thrasya*.

Materiales y Métodos

Se examinaron especímenes de los siguientes herbarios: B, BAA, BM, BR, COL, CTES, G, JUA, K, LIL, LPB, M, MEXU, MO, P, SI, US, VEN y W (Holmgren et al., 1990). Las especies *Thrasya achlysophila* Soderstr. [= *Paspalum achlysophilum* (Soderstr.) S. Denham], *T. parvula* A. G. Burm. [= *P. parvulum* (A. G. Burm.) S. Denham] y *T. schumannii* (Pilg.) Pilg. [= *P. schumannii* (Pilg.) S. Denham], sólo conocidas por el material tipo, y *T. seminuda* A. G. Burm. [= *P. seminudum* (A. G. Burm.) S. Denham], de la que existen escasas colecciones (Burman, 1985 [1987]), no pudieron localizarse en sus respectivos herbarios. No se observaron ejemplares de estas especies, pero se utilizó información de la bibliografía siempre que fue posible.

Para las especies previamente tratadas bajo el grupo informal Decumbentes se siguen los métodos de la taxonomía clásica. Para las especies previamente tratadas bajo el género *Thrasya*, no se realizaron descripciones; para estas especies se sigue el tratamiento de Burman (1985 [1987]), ya que las observaciones realizadas sobre material de herbario y plantas vivas en su hábitat coinciden con las descripciones de este autor. Sin embargo, se presenta una sinopsis para cada una de las especies que incluye la taxonomía completa, sinónimos actualizados, referencias a descripciones e iconografías, distribución geográfica y observaciones. Para cada especie se cita material representativo estudiado, y, en especies con escasas colecciones, se cita la totalidad de los ejemplares estudiados. En el Apéndice 2 se cita el material examinado completo en un índice de colecciones.

Para el estudio y la obtención de fotomicrografías de lemma y pálea del antecio superior se empleó un microscopio electrónico de barrido (MEB) Zeiss 940, perteneciente al Instituto de Botánica Darwinion (IBODA), Buenos Aires, Argentina, siguiendo el procedimiento descripto por Soderstrom y Zuloaga (1989). Los ejemplares utilizados para la observación de antecios al MEB se indican con dos asteriscos (**) en el Apéndice 2, excepto para *Paspalum peckii* F. T. Hubb. y *T. stricta* A. G. Burm. [= *P. huberi* S. Denham], especies en que se utilizaron los ejemplares tipo.

La metodología para los estudios histofoliares consistió en la obtención de cortes transversales y preparados epidérmicos de la lámina foliar y su posterior observación con microscopía óptica. En todos los casos posibles se utilizó un fragmento del tercio medio de la lámina de la segunda hoja de una innovación fértil. Los cortes transversales se realizaron a mano alzada, previo tratamiento con ácido fluorhídrico (HF) al 5% durante 24 horas. Para los preparados de epidermis se siguió el método de Metcalfe (1960). Los preparados fueron coloreados con safranina en solución acuosa y montados en gelatina-glicerina. Las observaciones anatómicas se realizaron con un microscopio fotónico Willd M20. Para la identificación de cuerpos silíceos se utilizó fenol líquido (Johansen, 1940); las células suberosas fueron puestas en evidencia mediante la técnica de coloración con Sudán III (Sass, 1940). Para las descripciones histofoliares se adoptó la terminología propuesta por Ellis (1976,

1979). Los ejemplares utilizados para el estudio histofoliar se indican con un asterisco (*) en el Apéndice 2, excepto para *P. peckii* y *T. stricta* (= *P. huberi*), especies en las que se utilizaron los ejemplares tipo.

Resultados

Sobre la base de los estudios filogenéticos de Denham y Zuloaga (en prensa) se transfieren las especies de *Thrasya* al género *Paspalum* y se establece el subgénero *Harpostachys* de *Paspalum* (véase Tratamiento Taxonómico) que incluye a las especies previamente tratadas bajo *Thrasya* y a las del grupo informal Decumbentes.

Las especies aceptadas en el subgénero *Harpostachys* de *Paspalum* se listan en el Apéndice 1.

Caracteres morfológicos

Hábito. Las especies del subgénero *Harpostachys* son principalmente perennes, sólo dos especies, *Paspalum axillare* y *P. carajasense*, son anuales. El subgénero comprende plantas cespitosas, con rizomas de entrenudos cortos más o menos plagiótropos, a estoloníferos en *P. petilum*, y cañas erectas o decumbentes, usualmente ramificadas (simples en *P. parvulum*, *P. thrasyoides*, *P. monostachyum* y *P. peckii*). *Paspalum monostachyum* y *P. unispicatum* se destacan por sus rizomas con zonas de entrenudos alargados entre dos zonas de entrenudos cortos, las porciones de rizoma con entrenudos alargados son arqueadas, cubiertas por catáfilos glabros o pilosos y lustrosos en *P. unispicatum*. Las cañas son huecas, de (12–)15–150 cm de alto, si bien en *P. foliiforme*, *P. cultratum* y *P. cinerascens* pueden alcanzar 160–200 cm. Los entrenudos son glabros o pilosos; la pilosidad de los nudos es variable, de glabros hasta pilosos o barbados.

Vainas y láminas. Las vainas, que pueden ser más cortas o más largas que los entrenudos, son glabras a pilosas, especialmente papiloso-pilosas, con los márgenes comúnmente pestañosos; en *P. cinerascens* las vainas pueden presentar densos pelos plateados y en *P. crucense* las vainas son glabras y con aurículas en el ápice. La lígula es membranácea, de 0.5–6 mm de largo; *P. subfalcatum* y *P. cultratum* se destacan por el escaso desarrollo de la lígula (0.5–0.7 mm de largo), mientras que en *P. crucense* alcanzan los 5 mm y en *P. seminudum* la lígula es de 5–6 mm de largo. Comúnmente está presente una seudolígula formada por un mechón de pelos, por detrás de la lígula, aunque ésta puede faltar. Las láminas son lineares o linear a linear-lanceoladas en la mayoría de las especies, de 2–68 cm de largo y 0.1–2(–2.4) cm de ancho; sin embargo, en *P. monostachyum* las láminas son filiformes y en *P. achlysophilum*, *P. scandens*, *P. nutans* y *P. variabile* son lanceoladas. Las láminas son planas o plegadas, con la base atenuada o redondeada y el ápice acuminado o agudo, glabras a pilosas o papiloso-pilosas, con los márgenes glabros o pestañosos. En *P. cultratum* las láminas se observan frecuentemente laciniadas.

Inflorescencias. Las especies del subgénero *Harpostachys* presentan inflorescencias terminales y axilares en la última vaina foliar (Fig. 1A); el número de inflorescencias axilares varía de 1–7 y en *P. decumbens* se pueden observar hasta 8 inflorescencias formando un sistema cimoso en la última vaina foliar. Es frecuente el desarrollo de inflorescencias subapicales en la caña floríferа. Los pedúnculos son glabros o pilosos, o densamente pilosos en la porción apical en *P. cultratum*; los pedúnculos terminales son comúnmente exertos, y los axilares subincluidos a incluidos. Las inflorescencias del grupo, como en la mayoría de las especies de *Paspalum*, son truncadas y homocládicas, formadas exclusivamente por paracladios largos (o racimos) (Rua & Weberling, 1995). El eje principal de la inflorescencia, cuando está presente, es aplanado a cilíndrico en *P. monostachyum*. Los pulvínulos son glabros a pilosos, en ocasiones con dos aurículas, de 0.5–4 mm de largo, que representan racimos proximales rudimentarios (Burman, 1985 [1987]; Rua & Weberling, 1995). Las especies del subgénero comúnmente presentan un racimo solitario por inflorescencia; no obstante algunas especies suelen presentar hasta dos racimos (*P. scandens* y *P. pilosum*), hasta tres (*P. oreophilum*, *P. seminudum* y *P. peckii*), hasta 4 racimos (*P. adoperiens*, *P. nutans* y *P. variabile*) o de uno a varios [9(16)] (*P. botterii*, *P. cinerascens* y *P. inconstans*). Los racimos se disponen sobre el eje de manera solitaria, alternos o menos frecuentemente subopuestos (*P. peckii*, *P. oreophilum* y *P. scandens*), con filotaxis dística. Los racimos, típicamente arqueados, tienen una longitud de 1–35 cm. El raquis de los racimos es triquetro o con extensiones laterales cortas, hasta foliáceo, de 0.3–7 mm de ancho y termina en una espiguilla desarrollada (paracladio heterotético, condición más frecuente en *Paspalum*) o en una extensión estéril (paracladio homotético o truncado); la superficie del raquis es glabra, o con pelos papilosos, dorados y patentes en *P. auricomum* o papilosos, pajizos y adpresos en *P. glaziovii*; los márgenes son glabros a densamente pilosos; en *P. monostachyum* los raquis de los racimos son triquetros a teretes. Los pedicelos se disponen en pares, cada par alternando a uno y otro lado de la

Figura 1. —A. *Paspalum decumbens.* Detalle del ápice de una caña florífera con tres pedúnculos en la última vaina foliar, con inflorescencias de racimos solitarios (de *Ferreyra 17178*). —B. *Paspalum thrasyoides.* Espiguilla mostrando la lemma inferior hendida con pelos conspicuos y rígidos hacia el ápice (de *Glaziou 20559*). —C. *Paspalum huberi.* Espiguilla, vista lateral mostrando la gluma superior más corta y más angosta que el antecio (de *Laegaard & Mayorga 17572*). —D. *Paspalum scandens.* Espiguilla mostrando la lemma inferior sulcada (de *Hook 804*). —E. *Paspalum inconstans.* Par de espiguillas (de *Barkly et al. 130*). —F. *Paspalum setosum.* Espiguilla, vista lateral mostrando antecio inferior y antecio superior (de *Wuddack & Monacino 39984*). —G. *Paspalum cultratum.* Espiguilla, vista lateral mostrando antecio inferior y antecio superior (de *Chase 1844*).

línea media del raquis o dispuestos sobre esta línea; los pedicelos de un par pueden ser subiguales en longitud o el superior estar elongado y ser marcadamente desigual; el pedicelo superior es libre o adnato al raquis; los pedicelos son principalmente glabros y escabrosos, no obstante suelen ser largamente ciliados en *P. monostachyum* y *P. parvulum.*

Espiguillas. Como en las Paniceas en general, las espiguillas del subgénero son bifloras, acrótonas, y sin extensión de la raquilla por encima del antecio superior, con la flor inferior neutra o estaminada y la superior perfecta. Las espiguillas se disponen en 2–4 series e imbricadas sobre el raquis o se ubican en 1 serie y parcialmente equidistantes, en este último arreglo puede no ser evidente la posición apareada de las mismas. Las espiguillas dispuestas en 2–4 series se disponen de manera que la espiguilla inferior y la espiguilla superior enfrentan su lemma inferior y gluma supe-

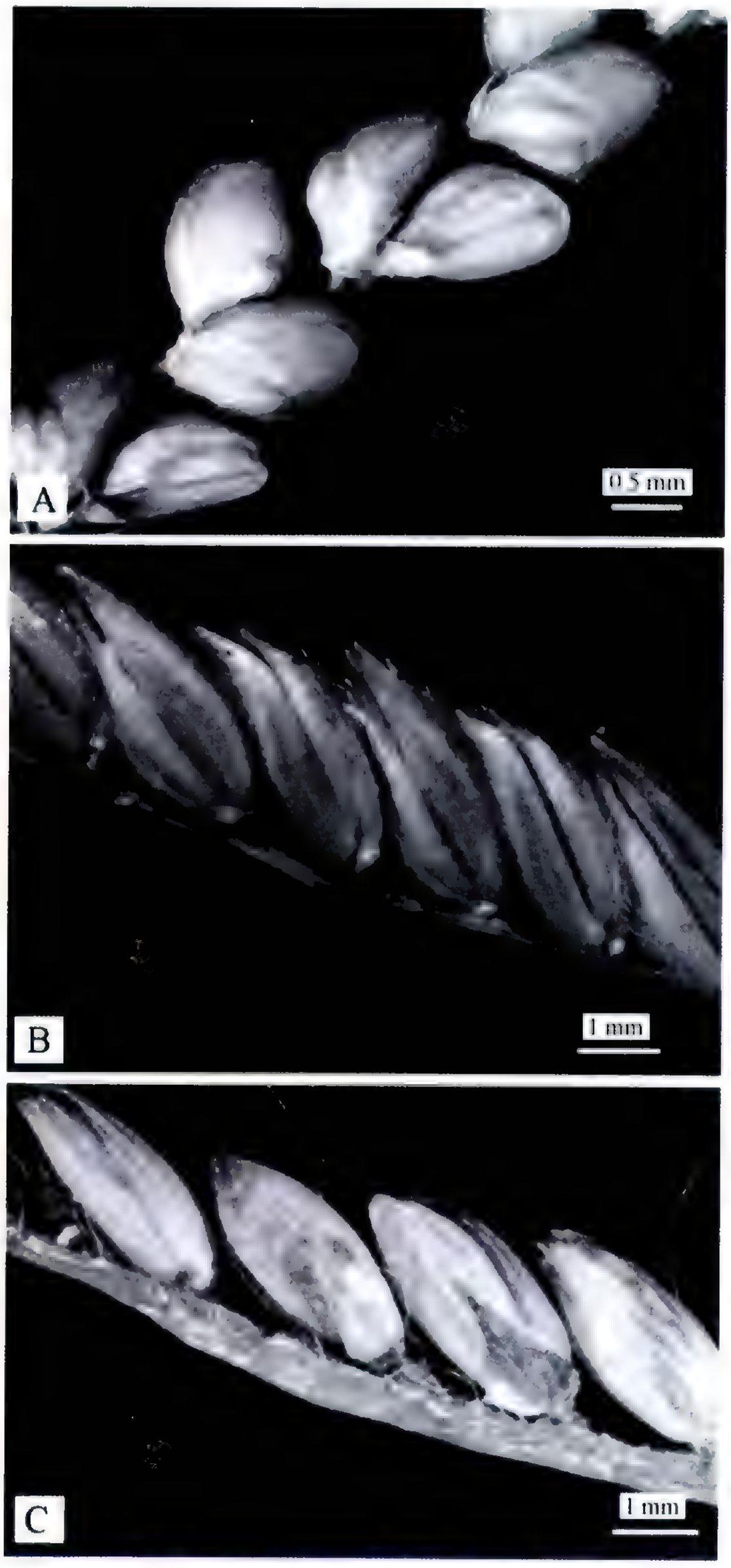

Figura 2. —A. *Paspalum decumbens*. Detalle del racimo con espiguillas dispuestas en posición "paspaloide" (de *Ferreyra 17247*). —B. *Paspalum trinitense*. Detalle del racimo con espiguillas dispuestas en posición "thrasyoide" (de *Soderstrom 997*). —C. *Paspalum oreophilum*. Detalle del racimo con espiguillas dispuestas en posición intermedia entre las posiciones "paspaloide" y "thrasyoide" (de *Irwin et al. 27989*).

rior, respectivamente, o la espiguilla inferior se ubica lateralmente con respecto a la superior (posición "paspaloide," Fig. 2A). En las espiguillas que se disponen en 1 serie y equidistantes, se enfrentan las lemmas inferiores de las espiguillas de un par (posición "thrasyoide," Fig. 2B). En *P. oreophilum*, *P. calliferum* y *P. cinerascens* la disposición de las espiguillas suele variar entre estos dos tipos de arreglos, incluso en un mismo racimo (Fig. 2C). La forma de las espiguillas es elipsoide a anchamente elipsoide en la mayoría de las especies; anchamente elipsoide a obovoides en *P. achlysophilum*, *P. nutans*, *P. hintonii*, *P. petilum* y *P. unispicatum*, obovoides en *P. decumbens* y suborbiculares en *P. adoperiens*. Las espiguillas son de 1.2–6 mm de largo y 0.6–1.9(–2) mm de ancho (la especie anual *P. axillare* presenta espiguillas muy pequeñas, de 0.9–1.1 mm de largo y 0.5 mm de ancho), dorsiventralmente comprimidas, plano-convexas a cóncavo-convexas, glabras a pilosas. *Paspalum glaziovii*, *P. orinocense*, *P. foliiforme*, *P. calliferum*, *P. setosum*, *P. axillare*, *P. crucense*, *P. carajasense*, *P. huberi*, *P. thrasyoides* y *P. trinitense* presentan un engrosamiento en la base de la espiguilla (Fig. 1B, C, F); Davidse (1987) confirma que los engrosamientos presentes en la base de las espiguillas de *P. foliiforme* son eleosomas, los que podrían relacionarse con la dispersión de las diásporas por hormigas (Morrone et al., 2000).

Gluma inferior. En las especies del subgénero *Harpostachys* la gluma inferior está presente en ambas o en una de las espiguillas del par, excluyendo *P. auricomum*, *P. axillare*, *P. glaziovii*, *P. orinocense* y *P. setosum*, especies en las que la gluma inferior es ausente en ambas espiguillas. En *P. inconstans* la gluma inferior es ausente en la espiguilla superior y presente o ausente en la inferior, mientras que en *P. monostachyum* la gluma inferior está ausente en la espiguilla inferior del par y ausente o presente en la superior; en *P. trinitense* y en *P. foliiforme* la gluma inferior sólo se desarrolla en la espiguilla inferior. En las restantes especies del grupo, la gluma inferior usualmente es dimorfa en las espiguillas superior e inferior de un par; frecuentemente en la espiguilla inferior es de mayor desarrollo (1/6 a subigual a la espiguilla), uninervia y excéntrica, mientras que en la espiguilla superior es más corta (1/6–1/2 de la espiguilla), enervia y centrada. La forma de la gluma es de base ancha y ápice obtuso, a triangular y ápice agudo o lanceolada a acuminada; es glabra o pilosa. En *P. variabile* la gluma inferior en la espiguilla superior del par es 2-nervia y con un amplio margen hialino, y en la espiguilla inferior es 3-nervia.

Gluma superior. La gluma superior es subigual a la espiguilla o ligeramente menor, sin embargo en *P. axillare*, *P. huberi*, *P. decumbens* y *P. hintonii* la gluma superior es 1/2 del largo de la espiguilla y en *P. schumannii* y *P. parvulum* es menor, hasta 1/3 de la misma. En *P. huberi*, *P. trinitense* y *P. thrasyoides* la gluma superior es más angosta que el antecio superior. Su consistencia es membranácea o papirácea, menos frecuentemente hialina (en

P. subfalcatum). La gluma superior es glabra, delicadamente pilosa, o con pelos conspicuos y rígidos; 3–7-nervia, aunque en *P. cinerascens* es 7–9-nervia, en *P. auricomum* 2-nervia y *P. axillare, P. parvulum* y *P. schumannii* presentan la gluma superior enervia. Los nervios son equidistantes o los marginales son próximos entre sí; en *P. dispar* y *P. unispicatum* los nervios son prominentes, mientras que en *P. cinerascens* y *P. oreophilum* son prominentes y con venillas transversales anastomosadas en el ápice, formando un retículo.

Lemma inferior. La lemma inferior es tan larga como la espiguilla, de consistencia cartácea, crustácea, papirácea, membranácea a hialina, con las células no distinguibles o con las paredes marcadas en *P. inconstans, P. monostachyum, P. nutans* y *P. petilum*; plana o sulcada, entera o hendida por el nervio medio; la superficie es lisa a finamente papilosa o papilosa en *P. cinerascens, P. cultratum, P. hintonii* y *P. pilosum.* La lemma inferior es glabra, pubescente o pilosa, con pelos en toda la superficie o especialmente sobre los nervios, en ocasiones con uno o dos pelos más largos que el resto; el ápice de la lemma inferior es retuso en *P. cultratum* y ocasionalmente retuso en *P. cinerascens.* La lemma inferior es (3)5–7-nervia, con los nervios equidistantes o los marginales próximos entre sí; los nervios son prominentes en *P. altsonii, P. dispar* y *P. hintonii* y prominentes y reticulados en el ápice en *P. cinerascens.* La lemma inferior abraza al antecio superior en su parte basal especialmente cuando la pálea y flor inferior son ausentes.

Pálea y flor inferior. Las especies del subgénero presentan la pálea inferior desarrollada, u ocasionalmente desarrollada, excluidas *P. parvulum, P. monostachyum, P. subfalcatum* y *P. variabile,* especies en las que no se observó esta bráctea. La pálea inferior, cuando presente, es usualmente hialina, excepto por los dos nervios endurecidos, es tan larga como la lemma o levemente más corta, a reducida en *P. botterii.* No se observó flor inferior en *P. achlysophilum, P. parvulum, P. axillare, P. trinitense, P. adoperiens, P. altsonii, P. botterii, P. monostachyum, P. petilum, P. subfalcatum* y *P. variabile*; en las restantes especies la flor inferior es estaminada, constituida por tres estambres, con anteras de 0.8–2.5 mm de largo (0.8 mm en *P. scandens* y 2.5 mm en *P. foliiforme* y *P. thrasyoides*).

Antecio superior. El antecio superior presenta la lemma con los bordes enrollados sobre la pálea; su forma varía de elipsoide a obovoide, suborbicular u ovado; mide de 1.2–5 mm de largo (5 mm en *P. foliiforme*) y 0.4–1.8 mm de ancho. El antecio es usualmente plano-convexo, aunque puede observarse cóncavo-convexo o bicóncavo; es crustáceo a membranáceo, pajizo o ferrugíneo en *P. glaziovii, P. botterii* y *P. variabile* o pajizo a grisáceo en *P. calliferum, P. cinerascens* y *P. cultratum*; el antecio puede ser glabro o con un mechón de pelos apicales, hasta de 1.5 mm de largo, los que se ubican principalmente sobre el dorso de la lemma. Los antecios presentan 2 lodículas membranáceas a hialinas de 0.1–0.6 mm de largo; tres estambres con anteras castañas, púrpuras o amarillas de 0.5–3 mm de largo (3 mm en *P. foliiforme*); el ovario presenta 2 estilos y el estigma es plumoso; la cariopsis es elíptica a suborbicular, de 0.6–2.5 mm de largo (2.5 mm en *P. oreophylum*) y 0.3–1.3 mm de ancho; el hilo es de forma linear, elíptico o suborbicular y mide 1/4–1/2 del largo de la cariopsis; el embrión es de 1/4–1/2 del largo de la cariopsis. En *P. auricomum, P. crucense, P. glaziovii, P. carajasense, P. scandens, P. thrasyoides, P. cinerascens, P. cultratum* y *P. peckii* no se observaron cariopsis.

Ornamentación del antecio superior (Fig. 3). La lemma y pálea presentan células cuadradas o rectangulares en vista superficial, con las paredes anticlinales onduladas. *Paspalum axillare, P. graniticum, P. petilum* y *P. subfalcatum* presentan papilas simples; sin embargo, las restantes especies presentan papilas verrugosas, distribuidas regularmente, con 2–12 verrugas en cada una (12 en *P. calliferum*). En *P. monostachyum* la pared tangencial de las células es no papilosa y lisa, mientras que en *P. dispar* es globosa. Es frecuente la presencia de micropelos bicelulares fusiformes, del tipo "panicoide," especialmente en el tercio superior y bordes de lemma y pálea, de 32–77 μm de largo, con la célula basal de paredes engrosadas y la distal de paredes delgadas, ambas de igual tamaño o la distal 1.5 o 2 veces más larga; en *P. dispar* se observaron micropelos con 2–5 células, hasta de 103 μm de largo. Se observaron macropelos unicelulares hacia el ápice de la lemma y pálea, de 50–172 μm de largo. En *P. graniticum, P. monostachyum* y *P. dispar* se observaron escasos cuerpos de sílice elípticos o cruciformes, exfoliados, dispuestos hacia los márgenes apicales de la lemma y pálea.

CARACTERES HISTOFOLIARES

Las especies del subgénero *Harpostachys* presentan una vaina Kranz con cloroplastos especializados alrededor de los haces vasculares. Anatómicamente pertenecen al subtipo MS (XyMS-) (Hattersley & Watson, 1976; Brown, 1977), especies caracterizadas por tener una única vaina alrededor de los haces vasculares en contacto directo con los vasos de metaxilema. Estos caracteres y la presencia de 1–3 células clorenquimáticas entre los haces, permite

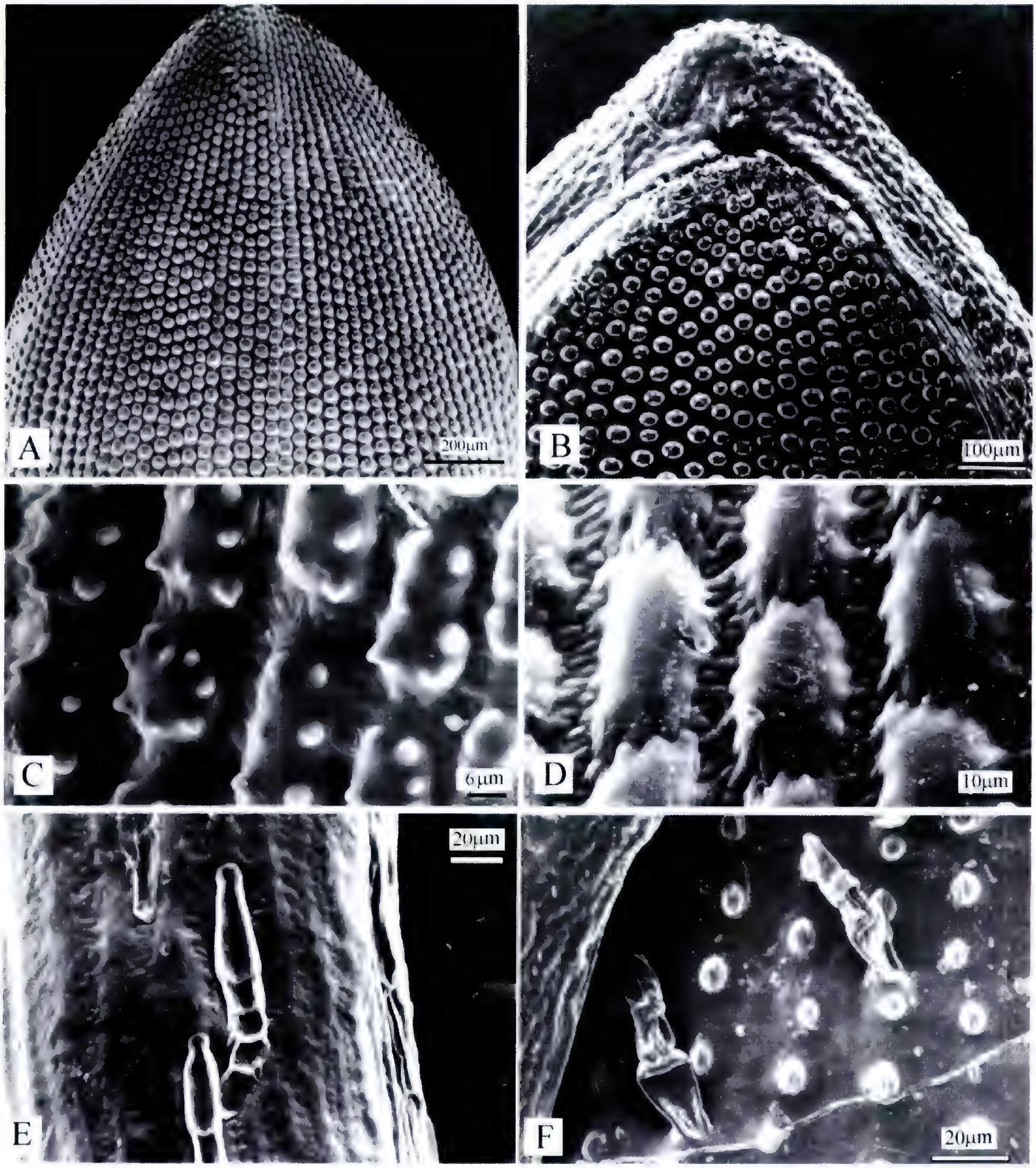

Figura 3. Fotomicrografías de antecios superiores de *Paspalum*. A, B. *Paspalum pilosum*. —A. Ápice del antecio superior visto del lado de la lemma (de *Irwin et al. 13764*). —B. Ápice del antecio superior visto del lado de la pálea (de *Davidse & González 19794*). —C. *Paspalum trinitense*. Pálea superior con papilas verrugosas (de *Soderstrom 981*). D, E. *Paspalum dispar*. —D. Lemma superior con células de paredes tangenciales globosas (de *Liogier 15976*). —E. Margen de la lemma superior vista del lado de la pálea, con micropelos de 5 células (de *Liogier 15976*). —F. *Paspalum subfalcatum*. Pálea superior con papilas simples y micropelos bicelulares (de *Liesner 17160*).

inferir que las especies estudiadas utilizan la vía fotosintética C_4, del subtipo NADP-me (Hattersley & Watson, 1976; Brown, 1977), como ocurre en las especies del género *Paspalum* en general.

Corte transversal (Fig. 4)

Transcorte. En la mayoría de las especies el transcorte es en forma de "V," con un ángulo desde 90º a expandido, con semiláminas simétricas, de 53–236 µm de espesor, con los márgenes rectos (a levemente revolutos en *P. foliiforme*, *P. scandens* y *P. nutans*) y con un número variable de haces de 1º orden. Los surcos y costillas son ausentes, leves o marcados por la presencia de casquetes de esclerénquima en las superficies abaxial y adaxial. *Paspalum monostachyum* se diferencia por presen-

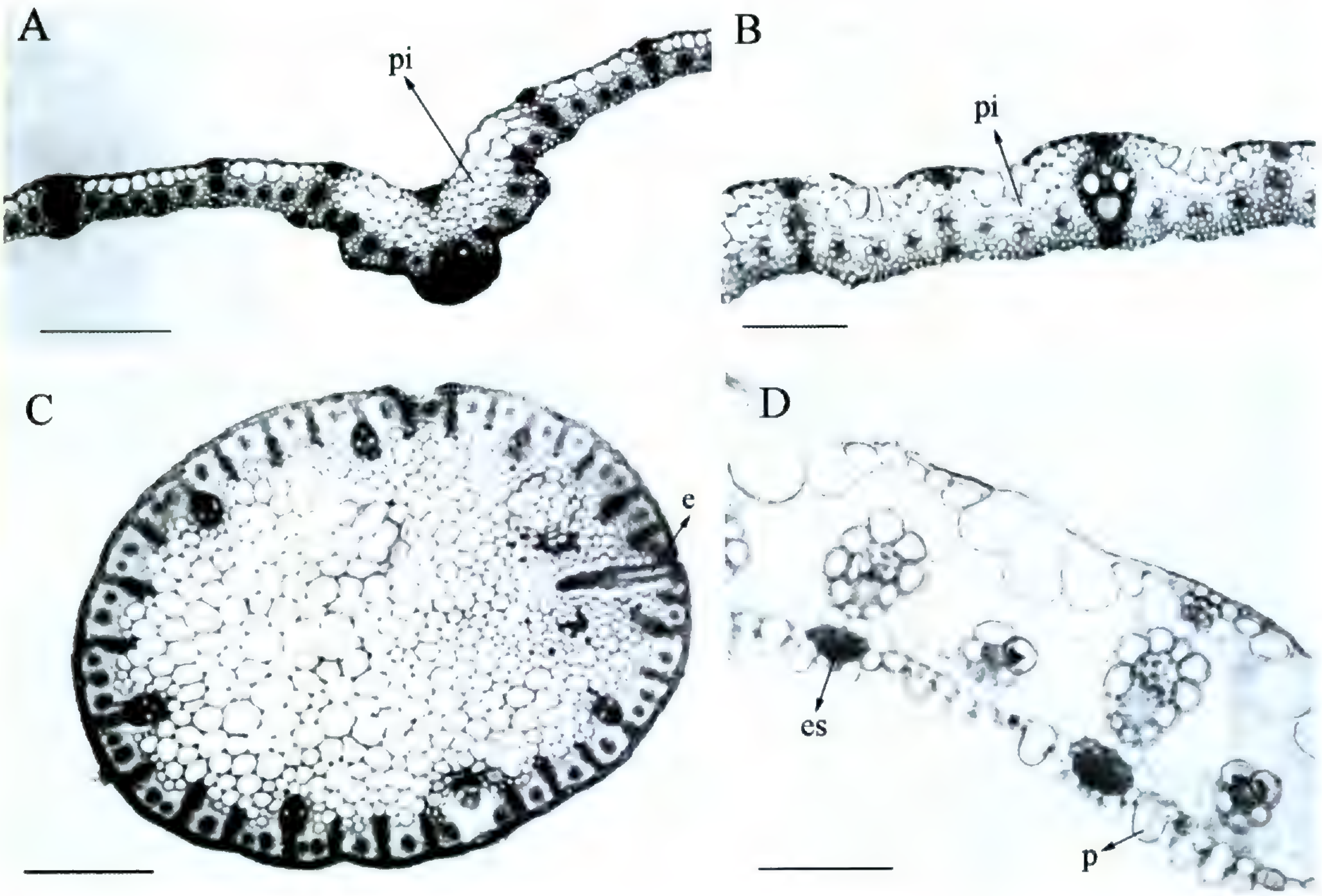

Figura 4. Transcortes foliares. —A. *Paspalum variabile*. Costilla central y porción de las semiláminas, parénquima incoloro (pi) asociado a la costilla central (de *Hitchcock 6439*). —B. *Paspalum cultratum*. Porción de la semilámina, mostrando parénquima incoloro (pi) asociado a las células buliformes (de *Chase 8651*). —C. *Paspalum monostachyum*. Transcorte elíptico con escotadura (e) en la cara adaxial (de *Rudolph 83*). —D. *Paspalum hintonii*. Porción de la semilámina, mostrando papilas (p) en la epidermis abaxial y casquetes de esclerénquima (es) (de *Santana et al. 2618*). Barra = 400 μm en A y C; 100 μm en B y D.

tar el corte transversal de contorno elíptico (2 × 1.6 mm aproximadamente) con una escotadura en la cara adaxial, con haces vasculares dispuestos periféricamente y una zona central ocupada por parénquima incoloro, de superficie adaxial reducida y abaxial lisa. En *P. orinocense*, *P. setosum* y *P. thrasyoides*, las semiláminas son revolutas; mientras que *P. auricomum* presenta un transcorte en forma de "U," con semiláminas muy cortas, de 260 μm de largo.

Costilla central. Estructuralmente distinguible, o inconspicua en *P. botterii*; con un número variable de células de parénquima incoloro distribuidas hacia la cara adaxial y con los haces vasculares desplazados hacia la cara abaxial; con 1–3 haces vasculares de 1º orden, (0)2–4(8) haces de 2º orden y 4–8(18) de 3º orden. La costilla central es aquillada en *P. axillare*, *P. adoperiens* y *P. subfalcatum*.

Distribución de los haces vasculares en las semiláminas. 1–8 haces vasculares de 2º orden y 4–8 haces de 3º orden entre dos haces de 1º orden consecutivos; los haces de 1º orden centrados en el transcorte, los de 2º orden centrados o abaxiales y los haces de 3º orden abaxiales y ubicados por debajo de las células buliformes.

Estructura de los haces vasculares. Haces vasculares de 1º orden de contorno elíptico, circular u obovado (oblato en *P. adoperiens* y *P. setosum*), con 2–4 vasos de metaxilema usualmente más anchos que las células de la vaina Kranz, en contacto directo con ella, de contorno angular o circular, con las paredes ligeramente engrosadas; protoxilema presente; tejido floemático en contacto o no con la vaina y comúnmente rodeado de tejido mecánico. Haces vasculares de 2º orden de contorno elíptico, circular u obovado, con xilema y floema distinguibles. Haces vasculares de 3º orden de contorno circular o elíptico, con xilema y floema distinguibles, excepto en *P. adoperiens*, *P. altsonii* y *P. botterii*.

Vainas de los haces. Haces vasculares de 1º orden rodeados por una vaina mestomática completa o interrumpida abaxialmente por esclerénquima, compuesta por células globosas o reniformes, con cloroplastos especializados de posición centrífuga; haces de 2º y 3º orden rodeados por una vaina continua; en los haces de 2º orden las células de

la vaina pueden ser todas isodiamétricas o las adaxiales de mayor tamaño que las abaxiales; extensiones de la vaina ausentes.

Esclerénquima. Discontinuo, de posición subepidérmica, escaso o formando trabas o casquetes abaxiales y adaxiales, relacionados a haces de 1º, 2º y 3º orden; esclerénquima presente en el margen de las láminas.

Mesófilo. Compacto, no radiado y con células clorenquimáticas isodiamétricas a irregularmente radiadas con células tubulares en la mitad adaxial de los haces; con 1–3 células clorenquimáticas entre haces vasculares contiguos. Células parenquimáticas incoloras asociadas a las células buliformes presentes en *P. cinerascens*, *P. cultratum*, *P. unispicatum*, *P. auricomum*, *P. procerum*, *P. foliiforme* y *P. calliferum*.

Epidermis adaxial en corte transversal. Células buliformes en grupos extensos de (4)7–16 células o en forma de abanico, con 3–8 células redondeadas, ocupando 1/3 a 1/2 del espesor del transcorte, dispuestas sobre los haces de 3º orden; al mismo nivel que las restantes células epidérmicas o levemente hundidas. Las restantes células epidérmicas adaxiales con pared tangencial externa recta o convexa, cutícula continua y de desarrollo variable. Macropelos ausentes o presentes, cuando presentes unicelulares, escasos a muy abundantes, asociados a células epidémicas en cojín o en el mismo nivel que el resto de las células epidérmicas.

Epidermis abaxial en corte transversal. Células epidérmicas de mayor tamaño que las adaxiales, de pared tangencial externa recta, convexa o papilosa, cutícula de escaso desarrollo. Macropelos ausentes o presentes, cuando presentes unicelulares, escasos a muy abundantes, asociados a células epidémicas en cojín o en el mismo nivel que el resto de las células epidérmicas.

Epidermis abaxial en vista topográfica (Fig. 5B, C, D)

Zonación. Zonas costales e intercostales distinguibles a levemente distinguibles. Zonas costales de 1–6 hileras de células de ancho y zonas intercostales de 2–11 hileras de células de ancho.

Células largas intercostales. De contorno rectangular, con paredes anticlinales longitudinales paralelas, onduladas a lisas y paredes anticlinales transversales rectas, raro oblicuas, y excavados en las interestomáticas.

Papilas. Ausentes o presentes, cuando presentes una por célula, ocupando toda la pared tangencial (en *P. altsonii*, *P. inconstans*, *P. nutans* y *P. pilosum*) o sólo parte de ella, excéntricas y con la pared engrosada.

Aguijones o ganchos. Ausentes o presentes, cuando presentes en las zonas costales o en las zonas costales e intercostales.

Micropelos. Bicelulares, de 40–75 µm de longitud, dispuestos en zonas intercostales, con la célula basal más corta que la distal, de paredes engrosadas y dispuesta por encima del nivel de las restantes células epidérmicas, y la apical de mayor longitud, de paredes delgadas y con el ápice agudo, generalmente caediza o colapsada. No se observaron micropelos en *P. auricomum* y *P. glaziovii*.

Macropelos. Ausentes o presentes, cuando presentes, de tipo unicelular, de estructura variable, de 100–700 µm de largo, con paredes gruesas, asociado a dos células epidérmicas o asociados a más de dos células epidérmicas sobreelevadas formando un cojín. En *P. subfalcatum* y en *P. pilosum* se observaron macropelos más largos, de 1700 y 1200 µm respectivamente, mientras que *P. thrasyoides* presenta pelos de diferente longitud, de 40–50 µm o de hasta 400 µm en la misma epidermis.

Cuerpos silíceos. Ausentes o presentes, cuando presentes, generalmente costales, nodulares o rectangulares, menos frecuentemente halteriformes, alternando con células largas o junto a células suberosas.

Células suberosas. Ausentes o presentes, cuando presentes rectangulares a cuadrangulares, en zonas costales o intercostales.

Aparatos estomáticos. De 20–55 µm de longitud y 13–40 µm de ancho, dispuestos en 1–4 hileras por zona intercostal, células subsidiarias en forma de domo o de contorno triangular, estomas consecutivos separados por 1–2 células interestomáticas.

Epidermis adaxial en vista topográfica (Fig. 5A)

Con características semejantes a la epidermis abaxial, diferenciándose de ésta por la presencia de células buliformes de contorno hexagonal, rectangular o cuadrangular, con paredes anticlinales longitudinales rectas, menos frecuentemente onduladas; con papilas ausentes y aparatos estomáticos ausentes o escasos.

Distribución y Hábitat

Las especies del subgénero *Harpostachys* de *Paspalum* son nativas de los trópicos y subtrópicos de América. Su distribución comprende desde el sur de los Estados Unidos de América, las Antillas y América Central, hasta la Argentina y Uruguay, desde aproximadamente los 33º de latitud Norte

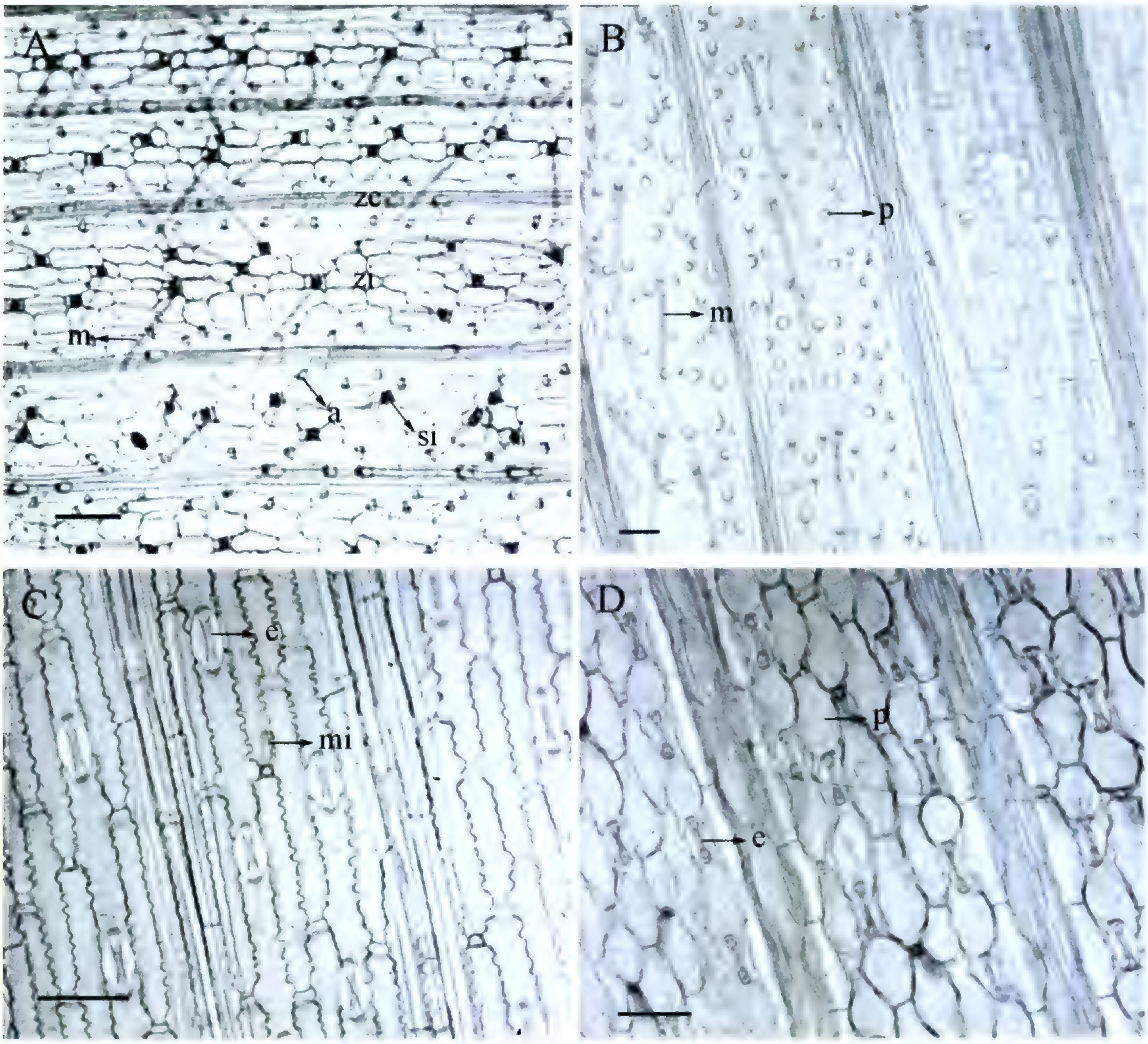

Figura 5. Epidermis en vistas topográficas. —A. *Paspalum graniticum*. Epidermis adaxial, zonas costales (zc) e intercostales (zi), macropelos (m), aguijones (a), y cuerpos silíceos (si) (de *Schulz & Donselaar 10581*). —B. *Paspalum procerum*. Epidermis abaxial, mostrando papilas (p) que ocupan sólo parte de la pared tangencial de la célula, excéntricas y con la pared engrosada, y macropelos (m) (de *Pittier 9517*). —C. *Paspalum dispar*. Epidermis abaxial, mostrando estomas (e) y célula basal de un micropelo (mi) (de *Ekman 13426*). —D. *Paspalum altsonii*. Epidermis abaxial, mostrando estomas (e) y papilas (p) que ocupan toda la pared tangencial de la célula epidérmica (de *Sandwith 1381*). Barra = 50 μm en A, B, C y D.

hasta los 32º de latitud Sur. El límite norte de distribución está establecido por *P. monostachyum* y *P. botterii*, y el límite austral por *P. unispicatum*. Las mayores concentraciones de especies se hallan en América central y norte de América del Sur, aunque también son abundantes en el sur y centro de Brasil. *Paspalum nutans* fue introducida en Mauricio, África (Smith et al., 1982; Pohl & Davidse, 1994).

Las especies de más amplia distribución son *P. pilosum*, *P. decumbens*, *P. foliiforme* y *P. campylostachyum*. Las dos primeras especies crecen desde México hasta el sur de Brasil, Perú y Bolivia, incluyendo islas del Caribe y Trinidad y Tobago; *P. foliiforme* habita desde Panamá a Brasil y Paraguay, aunque su distribución se extiende hasta México, donde es menos frecuente; finalmente, *P. campylostachyum* crece desde México a Bolivia.

Veintiuna de las 39 especies estudiadas son endémicas o de distribución restringida a un área de extensión reducida. Cinco especies son endémicas de los cerrados del sur de Brasil y Bolivia: *P. oreophilum* y *P. cultratum* en Minas Gerais; *P. seminudum* y *P. schumannii* en Mato Grosso; y *P. crucense* en Bolivia. La provincia fitogeográfica del Cerrado, del Dominio Amazónico, comprende bosques de escasa altura, arbustos y pastizales, también zonas elevadas con predomino de gramíneas (campos lim-

pios) y selva marginal a lo largo de arroyos y ríos (matas ciliares). Esta provincia presenta una precipitación anual intermedia (1200–2000 mm) y limita con la provincia Amazónica, con mayor humedad, y las provincias de la Caatinga y Chaqueña, más secas. Es característico del cerrado una marcada estación seca de mayo a septiembre y los suelos son pobres, usualmente profundos y lateríticos (Cabrera & Willink, 1973; Eiten, 1978; Navarro & Maldonado, 2002).

Nueve especies constituyen endemismos de un área que comprende a las Guayanas, sur de Venezuela, este de Colombia y noreste de Brasil, al norte de la provincia fitogeográfica Amazónica: *P. graniticum* (en Surinam), *P. scandens* (en las Guayanas), *P. achlysophilum* (en Guyana), *P. altsonii* (en Venezuela, Guyana y Surinam), *P. subfalcatum* (en sur de Venezuela y noreste de Brasil), *P. petilum* (en Guyana, sur de Venezuela y noreste de Brasil), *P. setosum*, *P. orinocense* (ambas en Venezuela, a orillas del Orinoco medio) y *P. huberi* (en el límite austral entre Venezuela y Colombia); éstas especies crecen preferentemente en los bordes de selva, frecuentemente en afloramientos rocosos, o sabanas del sur de Venezuela, las cuales se caracterizan por precipitaciones anuales de 2000–3000 mm y una leve estación seca en los meses de diciembre a marzo (Steyermark et al., 1995).

Paspalum parvulum, *P. carajasense* y *P. auricomum* crecen exclusivamente en Pará, Brasil. Finalmente, *P. hintonii* (en México), *P. mosquitiense* (en Honduras y Nicaragua), *P. peckii* (en Belize) y *P. dispar* (en la República Dominicana) crecen en áreas restringidas de América Central y Antillas, relacionadas a los ecosistemas boscosos, especialmente como componentes del sotobosque en pinares y encinares.

Paspalum inconstans presenta una distribución andina, desde Venezuela a Ecuador, Perú y Bolivia y crece entre los 800–3200 m de elevación.

Tres especies presentan un área de distribución disyunta: *P. nutans*, que crece al sur de México, América Central y Caribe, en Colombia, Venezuela, Guyana, Guayana Francesa y Ecuador y luego en Brasil, sobre la costa Atlántica; *P. adoperiens* en el norte de México y luego al sur de ese pais y Centro América; y *P. unispicatum* habita en Estados Unidos de América, México, Honduras, Cuba, norte de Venezuela y Ecuador, luego es muy frecuente desde Bolivia a Paraguay, Argentina y Uruguay, se encuentra también en Minas Gerais, Brasil.

Las especies del subgénero crecen principalmente desde el nivel del mar hasta los 2000 m de elevación, si bien *P. decumbens* alcanza 3180 m de elevación en Colombia y *P. inconstans*, especie exclusivamente andina, alcanza los 3200 m en Bolivia. Las especies del subgénero son frecuentes en los bordes de los bosques o en sus claros, en sabanas o en el cerrado. Crecen principalmente sobre suelos arenosos o rocosos, pero también en suelos arcillosos, de piedra caliza o volcánicos. Varias especies se desarrollan en áreas degradadas o en cultivos, especialmente en cafetales en México y América Central. *Paspalum monostachyum* y *P. nutans* pueden crecer en el litoral marítimo.

Los paises que presentan mayor número de especies son Venezuela (19 especies), Brasil (16 especies), México (11 especies), Colombia y Bolivia (10 especies) y Costa Rica y Honduras (9 especies). Brasil presenta el mayor número de endemismos por país, con seis especies que crecen exclusivamente en su territorio.

Tratamiento Taxonómico

Paspalum L., Syst. Nat., ed. 10, 2: 855. 1759. TIPO: *Paspalum dimidiatum* L., nom. illeg. superfl. [= *Paspalum dissectum* (L.) L.] (lectotipo, designado por Chase (Proc. Biol. Soc. Washington 24: 137. 1911)).

Ceresia Pers., Syn. Pl. 1: 85. 1805. TIPO: *Ceresia elegans* Pers. [= *Paspalum ceresia* (Kunth) Chase].

Reimaria Flüggé, Gram. Monogr., Paspalum: 213. 1810. TIPO: *Reimaria candida* (Kunth) Flüggé [= *Paspalum candidum* Kunth].

Thrasya Kunth, Nov. Gen. Sp. 1: 120–121. 1815[1816]. *Panicum* sect. *Thrasya* (Kunth) Benth., J. Linn. Soc., Bot. 18: 42. 1881. TIPO: *Thrasya paspaloides* Kunth [= *Paspalum orinocense* S. Denham].

Paspalanthium Desv., Opusc. Sci. Phys. Nat.: 59. 1831. TIPO: *Paspalanthium stoloniferum* (Bosc.) Desv. [= *Paspalum racemosum* Lam.].

Anachyris Nees, Hooker's J. Bot., Kew Gard. Misc. 2: 103. 1850. TIPO: *Anachyris paspaloides* Nees [= *Paspalum malacophyllum* Trin.].

Dimorphostachys E. Fourn., Compt. Rend. Acad. Sci. Paris 80: 441. 1875. TIPO: *Dimorphostachys monostachya* (Kunth) E. Fourn. [= *Paspalum pilosum* Lam.] (lectotipo, designado por Hitchcock (U.S.D.A. Bull. 772: 227. 1920)).

Tylothrasya Döll, Fl. Bras. 2: 295. 1877. TIPO: *Tylothrasya petrosa* (Trin.) Döll. [= *Paspalum foliiforme* S. Denham].

Plantas anuales o perennes, cespitosas, estoloníferas o rizomatosas. *Lígulas* membranáceas; *láminas* lanceoladas, lineares a filiformes, planas a conduplicadas, de pilosidad variable. *Inflorescencias* formadas por 1 a numerosos racimos unilaterales, solitarios, en pares o en panojas racemosas; raquis de los racimos triquetro a plano, estrecho a anchamente foliáceo; espiguillas solitarias o en pares, subsésiles a cortamente pediceladas, distribuidas en (1)2–4 series, desarticulando por debajo de las glumas junto a la inserción con el pedicelo. *Espiguillas* elipsoides u obovoides hasta orbicular-

es, dorsiventralmente comprimidas, plano-convexas a cóncavo-convexas, 2-floras; *gluma inferior* ausente, menos frecuentemente presente, cuando presente menor a la gluma superior; *gluma superior* presente, tan larga como la espiguilla o menor, en ocasiones ausente; *lemma inferior* presente, tan larga como la espiguilla; *pálea inferior* presente o ausente; *flor inferior* neutra, en ocasiones estaminada; *antecio superior* perfecto, de consistencia variable, de hialino a membranáceo o crustáceo, pajizo a castaño oscuro o negruzco a la madurez, liso a papiloso; lemma usualmente con los márgenes enrollados sobre la pálea, con el dorso dispuesto contra el raquis; pálea de igual tamaño y consistencia que la lemma; estambres 3; estigmas plumosos. *Cariopsis* con hilo usualmente punctiforme; embrión 1/2 o menos del largo de la cariopsis. Número cromosómico básico, $x = 10$.

Clave para Diferenciar a los Subgéneros de *Paspalum*

1. Espiguillas naviculares; lemma superior surcada por 5 nervios prominentes; gluma superior usualmente ausente ..... *Paspalum* subg. *Anachyris* Chase
1′. Espiguillas plano-convexas o cóncavo-convexas, no naviculares; lemma superior lisa, con nervios indistinguibles; gluma superior usualmente presente 2
2(1). Antecio superior hialino a membranáceo, ápice de la pálea superior libre; raquis de los racimos usualmente foliáceo y con el borde hialino; espiguillas generalmente densamente pilosas ..... *Paspalum* subg. *Ceresia* (Pers.) Rchb.
2′. Antecio superior cartáceo o crustáceo, menos frecuentemente membranáceo, ápice de la pálea superior encerrado por la lemma; raquis de los racimos usualmente triquetro o foliáceo pero sin el borde hialino; espiguillas glabras o pilosas 3
3(2). Gluma inferior usualmente presente y dimorfa en las espiguillas de un par; pálea inferior generalmente presente; pedúnculos terminales y axilares presentes en la última vaina foliar ..... *Paspalum* subg. *Harpostachys* (Trin.) S. Denham
3′. Gluma inferior generalmente ausente, cuando presente isomorfa en todas las espiguillas; pálea inferior generalmente ausente; pedúnculos solitarios en la última vaina foliar ..... *Paspalum* subg. *Paspalum*

Paspalum subg. **Harpostachys** (Trin.) S. Denham, comb. nov. Basónimo: *Panicum* sect. *Harpostachys* Trin., Mém. Acad. Imp. Sci. Saint-Petersbourg, Math., Seconde Pt. Sci. Nat. 3(2): 194, 227. 1834. *Panicum* subg. *Harpostachys* (Trin.) Hack., Oesterr. Bot. Z. 51: 367. 1901. TIPO: *Panicum decumbens* (Sw.) Roem. & Schult. [= *Paspalum decumbens* Sw.] (lectotipo, designado aquí).

Thrasya Kunth, Nov. Gen. Sp. 1: 120–121. 1815[1816]. *Panicum* sect. *Thrasya* (Kunth) Benth., J. Linn. Soc., Bot. 18: 42. 1881. TIPO: *Thrasya paspaloides* Kunth [= *Paspalum orinocense* S. Denham].

Dimorphostachys E. Fourn., Compt. Rend. Acad. Sci. Paris 80: 441. 1875. TIPO: *Dimorphostachys monostachya* (Kunth) E. Fourn. [= *Paspalum pilosum* Lam.] (lectotipo, designado por Hitchcock (U.S.D.A. Bull. 772: 227. 1920)).

Tylothrasya Döll, Fl. Bras. 2: 295. 1877. TIPO: *Tylothrasya petrosa* (Trin.) Döll. [= *Paspalum foliiforme* S. Denham].

Paspalum grupo Decumbentes Chase, Contr. U.S. Natl. Herb. 28: 91. 1929.

Plantas perennes, raro anuales, cespitosas, cañas erectas a decumbentes. *Láminas* lineares o linear a linear-lanceoladas, menos frecuentemente filiformes o lanceoladas. *Inflorescencias* terminales y axilares en la última vaina foliar, racimos usualmente solitarios, en ocasiones 2–varios racimos, raquis de los racimos triquetro o foliáceo. *Espiguillas* plano-convexas o cóncavo-convexas, pareadas, dispuestas en 2–4 series, imbricadas sobre el raquis o en una serie y equidistantes; *gluma inferior* usualmente presente y dimorfa en las espiguillas de un par; *lemma inferior* plana o sulcada, entera o hendida por el nervio medio; *pálea y flor inferior* usualmente presentes; *antecio superior* glabro o con un mechón de pelos apicales, lemma y páleas con papilas verrugosas en la superficie, menos frecuentemente con papilas simples o la superficie lisa.

Subgénero integrado por 39 especies, distribuidas en áreas tropicales y subtropicales de América, desde Estados Unidos de América hasta la Argentina y Uruguay, con especies en islas del Caribe y Trinidad y Tobago. Una especie introducida en el Viejo Mundo.

Trinius (1834) no designa una especie tipo para la sección *Harpostachys*. Aquí se designa a *Panicum decumbens* [= *Paspalum decumbens*] como lectotipo porque las características de esta especie coinciden con la descripción de *Panicum* sect. *Harpostachys* [= *Paspalum* subg. *Harpostachys*].

Clave para Diferenciar a las Especies del Subgénero *Harpostachys* de *Paspalum*

1a. Lemma inferior con pelos conspicuos y rígidos sobre los nervios y especialmente hacia el ápice (Fig. 1B).
  2a. Raquis de los racimos con los márgenes y la superficie adaxial con pelos papilosos, dorados y patentes a la superficie del raquis ..... 4. *P. auricomum*
  2b. Raquis de los racimos con la superficie adaxial glabra y los márgenes glabros o pilosos con pelos no

dorados (*P. glaziovii* puede presentar pelos en la superficie del raquis, pero éstos son adpresos a la superficie).

3a. Gluma superior más corta (1/2–2/3 del largo del antecio) y más angosta que el antecio superior (Fig. 1C).
- 4a. Gluma superior glabra y acuminada; márgenes del raquis glabros ..... 19. *P. huberi*
- 4b. Gluma superior pilosa y obtusa; márgenes del raquis pilosos.
  - 5a. Espiguillas de 2.4–2.6 mm de largo; plantas de 25–35 cm de alto; cañas ramificadas; láminas de 2–5 cm de largo; racimos de 1.5–6 cm de largo ..... 37. *P. trinitense*
  - 5b. Espiguillas de 3–4 mm de largo; plantas de 30–100 cm de alto; cañas simples; láminas de 4–15 cm de largo; racimos de 4–12 cm de largo ..... 36. *P. thrasyoides*

3b. Gluma superior de igual largo o mayor que el antecio superior y de igual ancho (Fig. 1F).
- 6a. Gluma superior y antecio superior más cortos que la lemma inferior, o gluma, lemma y antecio del mismo largo.
  - 7a. Vainas foliares glabras, con aurículas en el ápice ..... 10. *P. crucense*
  - 7b. Vainas foliares pilosas, sin aurículas.
    - 8a. Gluma inferior ausente; espiguillas de 2.7–3.5 mm de largo; racimos 1, de 8–13 cm de largo ..... 16. *P. glaziovii*
    - 8b. Gluma inferior presente; espiguillas de 3.5–4 mm de largo; racimos 1–3, de 14–30 cm de largo ..... 33. *P. seminudum*
- 6b. Gluma superior y lemma inferior más largas que el antecio.
  - 9a. Cañas decumbentes a postradas; raquis de los racimos con el margen glabro; gluma superior con escasos pelos conspicuos hacia el ápice, en ocasiones glabra ..... 34. *P. setosum*
  - 9b. Cañas erectas; raquis de los racimos con el margen piloso, con pelos delicados, no papilosos; gluma superior densamente pilosa en toda la superficie ..... 25. *P. orinocense*

1b. Lemma inferior glabra o con pelos delicados o conspicuos, pero distribuidos regularmente sobre la superficie, no exclusivamente sobre los nervios.

10a. Plantas anuales.
- 11a. Espiguillas 0.9–1.1 mm de largo; gluma inferior ausente; gluma superior 1/2 del largo de la espiguilla ..... 5. *P. axillare*
- 11b. Espiguillas 2–2.5 mm de largo; gluma inferior presente; gluma superior subigual a la espiguilla ..... 8. *P. carajasense*

10b. Plantas perennes.
- 12a. Láminas filiformes; raquis de los racimos triquetro o terete; rizomas con zonas de entrenudos alargados ..... 21. *P. monostachyum*
- 12b. Láminas planas o plegadas; raquis de los racimos triquetro, con cortas extensiones laterales o foliáceos; rizomas con entrenudos cortos (o con zonas de entrenudos alargados en *P. unispicatum*, pero con láminas planas a plegadas y racimos triquetros).
  - 13a. Gluma superior con venillas anastomosadas en la porción apical.
    - 14a. Raquis de los racimos foliáceo, de 2–2.5 mm de ancho, con los márgenes pilosos, con pelos papilosos, dorados, hasta de 8 mm de largo (Fig. 2C) ..... 24. *P. oreophilum*
    - 14b. Raquis de los racimos triquetro, de 0.7–1 mm de ancho, con los márgenes glabros o pilosos, con pelos no dorados, de 2–4 mm de largo ..... 9. *P. cinerascens*
  - 13b. Gluma superior sin venillas anastomosadas en la porción apical.
    - 15a. Raquis de los racimos con el margen regularmente piloso, con pelos papilosos, rígidos y dorados ..... 32. *P. schumannii*
    - 15b. Raquis de los racimos con el margen glabro o esparcidamente ciliado, pero con pelos no dorados.
      - 16a. Espiguillas dispuestas en posición "thrasyoide" ("back to back") sobre el raquis (raro algunas espiguillas del racimo de posición "paspaloide" en *P. calliferum*).
        - 17a. Lemma inferior glabra (raro ciliada en *P. campylostachyum*).
          - 18a. Lemma inferior membranácea o membranácea a hialina.
            - 19a. Gluma superior escuamiforme, 1/6–1/3 del largo de la espiguilla, enervia ..... 26. *P. parvulum*
            - 19b. Gluma superior 1/2–1/1 del largo de la espiguilla, 3–7-nervia.
              - 20a. Plantas hasta de 25 cm de alto; cañas erectas; racimos de 2–3 cm de largo; gluma superior 7-nervia ..... 1. *P. achlysophilum*
              - 20b. Plantas de 70–100 cm de alto; cañas decumbentes; racimos de 4–11 cm de largo; gluma superior 3–5-nervia ..... 31. *P. scandens*
          - 18b. Lemma inferior endurecida, cartácea.
            - 21a. Racimos 1–4, de 0.9–1.1 mm de ancho; espiguillas de 2.4–2.6 mm de largo, hasta de 0.7 mm de ancho; lemma inferior 5-nervia ..... 17. *P. graniticum*
            - 21b. Racimos 1, de 1.8–2.8 mm de ancho; espiguillas de 2.7–4 mm de largo, 0.8–1.8 mm de ancho; lemma inferior 7-nervia.

22a. Racimos de 4–10 cm de largo, 1.8–2 mm de ancho; espiguillas de 2.7–3 mm de largo, 0.8–1 mm de ancho ..... 7. *P. campylostachyum*

22b. Racimos de 10–16 cm de largo, 2.6–2.8 mm de ancho; espiguillas de 3.4–4 mm de largo, 1.4–1.8 mm de ancho ..... 22. *P. mosquitiense*

17b. Lemma inferior pilosa.

23a. Gluma superior de ápice acuminado, con pelos blanquecinos, más abundantes hacia la mitad inferior; raquis de los racimos de 15–35 cm de largo, 4–7 mm de ancho (a la madurez el raquis se observa enrollado a lo largo) ..... 15. *P. foliiforme*

23b. Gluma superior de ápice agudo, con pelos pajizos en toda la superficie; raquis de los racimos de 8–30 cm de largo, 2.5–3 mm de ancho ..... 14. *P. calliferum*

16b. Espiguillas en posición "paspaloide" sobre el raquis (Fig. 2A).

24a. Lemma inferior con ápice retuso ..... 11. *P. cultratum*

24b. Lemma inferior con ápice no retuso 25

25a. Gluma superior y lemma inferior glabras (ocasionalmente ciliolada en los márgenes de la gluma superior en *P. nutans*, entonces con la gluma inferior ausente en practicamente todas las espiguillas).

26a. Lemma inferior sulcada.

27a. Rizomas con zonas de entrenudos largos, delgados y arqueados ..... 38. *P. unispicatum*

27b. Rizomas de entrenudos cortos.

28a. Espiguillas de 3.2–3.5 mm de largo ..... 30. *P. procerum*

28b. Espiguillas de (2.2–)2.4–3 mm de largo.

29a. Racimos 2–3, de 1.9 mm de ancho; espiguillas elipsoides, de 2.5–2.7 mm de largo, 1.2–1.3 mm de ancho ..... 27. *P. peckii*

29b. Racimos 1, raro 2, de 0.8–1.5 mm de ancho; espiguillas anchamente elipsoides, de (2.2–)2.4–3 mm de largo, 1.5–1.8 mm de ancho ..... 29. *P. pilosum*

26b. Lemma inferior plana, no sulcada.

30a. Gluma inferior usualmente ausente, cuando presente sólo en unas pocas espiguillas de un racimo.

31a. Gluma superior 1/2 de la espiguilla; lemma inferior cartácea, papilosa, con los nervios laterales endurecidos, prominentes; láminas lineares ..... 18. *P. hintonii*

31b. Gluma superior 3/4 o más de la espiguilla; lemma inferior membranácea a papirácea, no papilosa, con los nervios no endurecidos; láminas lanceoladas ..... 23. *P. nutans*

30b. Gluma inferior presente en practicamente todas las espiguillas de un racimo.

32a. Racimos 2–3 por inflorescencia ..... 27. *P. peckii*

32b. Racimos 1 por inflorescencia.

33a. Cañas apoyantes a decumbentes; láminas lanceoladas a linear-lanceoladas, de 3.5–8(–10) cm de largo, 0.4–1 cm de ancho; espiguillas obovoides, de 1.2–1.8 mm de largo, 1–1.1 mm de ancho ..... 12. *P. decumbens*

33b. Cañas erectas; láminas lineares, de 5–30 cm de largo, 0.3–0.6 cm de ancho; espiguillas anchamente elipsoides, de 1.9–2 mm de largo, 1.2–1.3 mm de ancho ..... 13. *P. dispar*

25b. Gluma superior pilosa o ciliolada, con pelos delicados (raro la gluma superior glabra en algunas espiguillas de un racimo); lemma inferior glabra a pilosa con pelos delicados.

34a. Gluma inferior 2-nervia, con un amplio margen hialino en la espiguilla superior del par y 3-nervia en la espiguilla inferior ..... 39. *P. variabile*

34b. Gluma inferior 0–1-nervia, sin amplio margen hialino.

35a. Espiguillas suborbiculares; pulvínulos con dos aurículas ..... 2. *P. adoperiens*

35b. Espiguillas elipsoides, anchamente o largamente elipsoides o obovoides; pulvínulos sin aurículas.

36a. Racimos de 1–3(–4) cm de largo, que no sobrepasan la altura de las láminas; espiguillas de 1.4–2 mm de largo ..... 28. *P. petilum*

36b. Racimos de 3–18 cm de largo, que sobrepasan la altura de las láminas; espiguillas de 2–3.5 mm de largo.

37a. Racimos 1, raro 2.

38a. Espiguillas de 3.2–3.5 mm de largo; racimos de 7–18 cm de largo, 1.5–2 mm de ancho ..... 30. *P. procerum*

38b. Espiguillas de 2–2.8(–3) mm de largo; racimos de 3–7(–8) cm de largo, 0.4–0.9 mm de ancho.

39a. Gluma superior ciliolada en los márgenes basales y medios o junto al ápice; lemma inferior cartácea, suavemente sulcada, con los nervios marcados, glabra a escasamente pilosa en los márgenes ..... 3. *P. altsonii*

39b. Gluma superior pubescente en los márgenes y en la superficie; lemma inferior papirácea a hialina, plana a convexa, con los nervios no marcados, pubescente ..... 35. *P. subfalcatum*

37b. Racimos 1–9(16).

40a. Espiguillas elipsoides a ligeramente obovoides, maculadas o con manchas glandulares, pilosas, con pelos distribuidos en toda la superficie de la gluma superior; lemma inferior glabra a esparcidamente pubescente ..... 6. *P. botterii*

40b. Espiguillas largamente elipsoides, verdosas, pálidas o con tintes violáceos, gluma superior ciliolada especialmente sobre los márgenes; lemma inferior glabra ..... 20. *P. inconstans*

Especies Incluidas en el Subgénero *Harpostachys* de *Paspalum*

1. Paspalum achlysophilum (Soderstr.) S. Denham, comb. nov. Basónimo: *Thrasya achlysophila* Soderstr., Mem. New York Bot. Gard. 12(3): 4. 1965. TIPO: Guyana. Kaeiteur Plateau, 13 Mar. 1962, *R. S. Cowan & T. R. Soderstrom 2166* (holotipo, US no visto, foto SI!; isotipos, K no visto, NY no visto).

Referencias. Para descripción de la especie véase Burman (1985 [1987]); esta especie no ha sido ilustrada.

Distribución y ecología. Paspalum achlysophilum es endémica de Guyana (Fig. 6), donde crece formando matas sobre suelos húmedos.

Observaciones. Esta especie es sólo conocida por el material tipo, el cual no fue localizado (sólo se observó foto del holotipo). Se caracteriza por su lemma inferior membranácea, sulcada y por la escasa altura de las matas (hasta de 25 cm), con cañas erectas; los racimos solitarios miden 2–3 cm de largo, las láminas son lanceoladas, las espiguillas anchamente elipsoides a obovoides y la gluma superior es 7-nervia. La pálea y flor inferior son ausentes. La posición "thrasyoide" de las espiguillas sobre el raquis y la lemma sulcada relacionan a *P. achlysophilum* con las restantes especies del subgénero *Harpostachys* y, dentro de éste, se relaciona con *P. parvulum* y *P. scandens* por la consistencia membranácea o hialina de la lemma inferior.

2. Paspalum adoperiens (E. Fourn.) Chase, Contr. U.S. Natl. Herb. 28(1): 102. 1929. *Dimorphostachys adoperiens* E. Fourn., Mexic. Pl. 2: 15. 1886. TIPO: México. Veracruz: Orizaba, *J. G. Schaffner 271* (holotipo, P!; isotipos, NY no visto, US-865867!). Figura 7.

Paspalum culiacanum Vasey, Contr. U.S. Natl. Herb. 1(8): 281. 1893. Syn. nov. TIPO. México. Sinaloa: Culiacán, 1891, *E. Palmer 1647* (holotipo, US-471366!, foto SI!; isotipo, US-471367!).

Paspalum guatemalense Bartlett, Proc. Amer. Acad. Arts 43(2): 49. 1907. TIPO: Guatemala. Zacapa: Gualan,

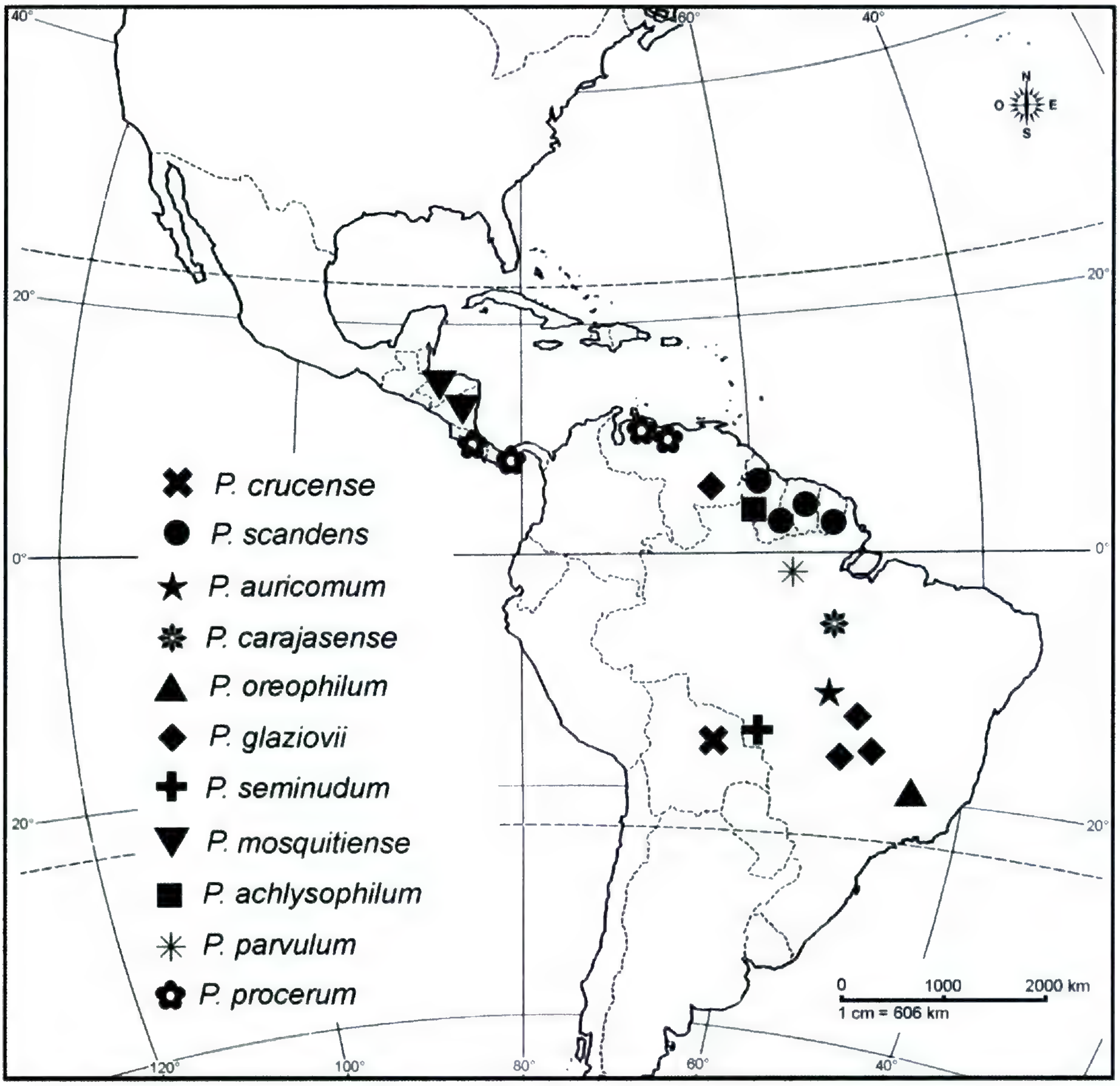

Figura 6. Distribución de *Paspalum crucense, P. scandens, P. auricomum, P. carajasense, P. oreophilum, P. glaziovii, P. seminudum, P. mosquitiense, P. achlysophilum, P. parvulum* y *P. procerum.*

C. C. Deam 427 (holotipo, GH no visto; isotipo, US-2855319!).

Plantas perennes, cespitosas, con rizomas de entrenudos cortos; *cañas* de 35–95 cm de alto, 2–3 mm de diámetro, erectas a decumbentes, ramificadas en los nudos inferiores y medios; entrenudos de 8–20 cm de largo, comprimidos, glabros; nudos glabros a pilosos, castaños a negruzcos. *Vainas* de 7–16 cm de largo, glabras o esparcidamente pilosas o papiloso-pilosas hacia la porción distal, luego glabras, los márgenes glabros o pestañosos; *lígulas* membranáceas, de 2–4 mm de largo; seudolígula formada por pelos de 4–5 mm de largo; cuello piloso; *láminas* lanceoladas a linear-lanceoladas, de 6–20 cm de largo, 0.6–1.5 mm de ancho, herbáceas, planas, de base angostada a redondeada, de ápice agudo, glabras a pilosas en ambas caras o sólo la abaxial, nervio medio conspicuo. *Pedúnculos* 1–3 en la última vaina foliar, subincluidos a exertos, hasta de 25 cm de largo, filiformes, glabros; comúnmente con pedúnculos incluidos en las vainas subapicales y ocasionalmente en las vainas medias. *Inflorescencias* terminales y axilares; racimos (1)2–4, alternos, divergentes del eje principal; eje principal nulo o hasta de 7 cm de largo, glabro, acanalado; pulvínulos glabros a pilosos, con dos aurículas pequeñas; raquis de los racimos de 2–9.5 cm de largo, 0.5–1 mm de ancho, triquetro, glabro o con escasos pelos en los márgenes, terminando en una espiguilla desarrollada; pedicelos en pares, escabrosos, desiguales, el de la espiguilla superior hasta de 1.5 mm de largo; espiguillas imbricadas, irregularmente dispuestas en 2–4 series, en ocasiones la inferior reducida. *Espiguillas* suborbiculares,

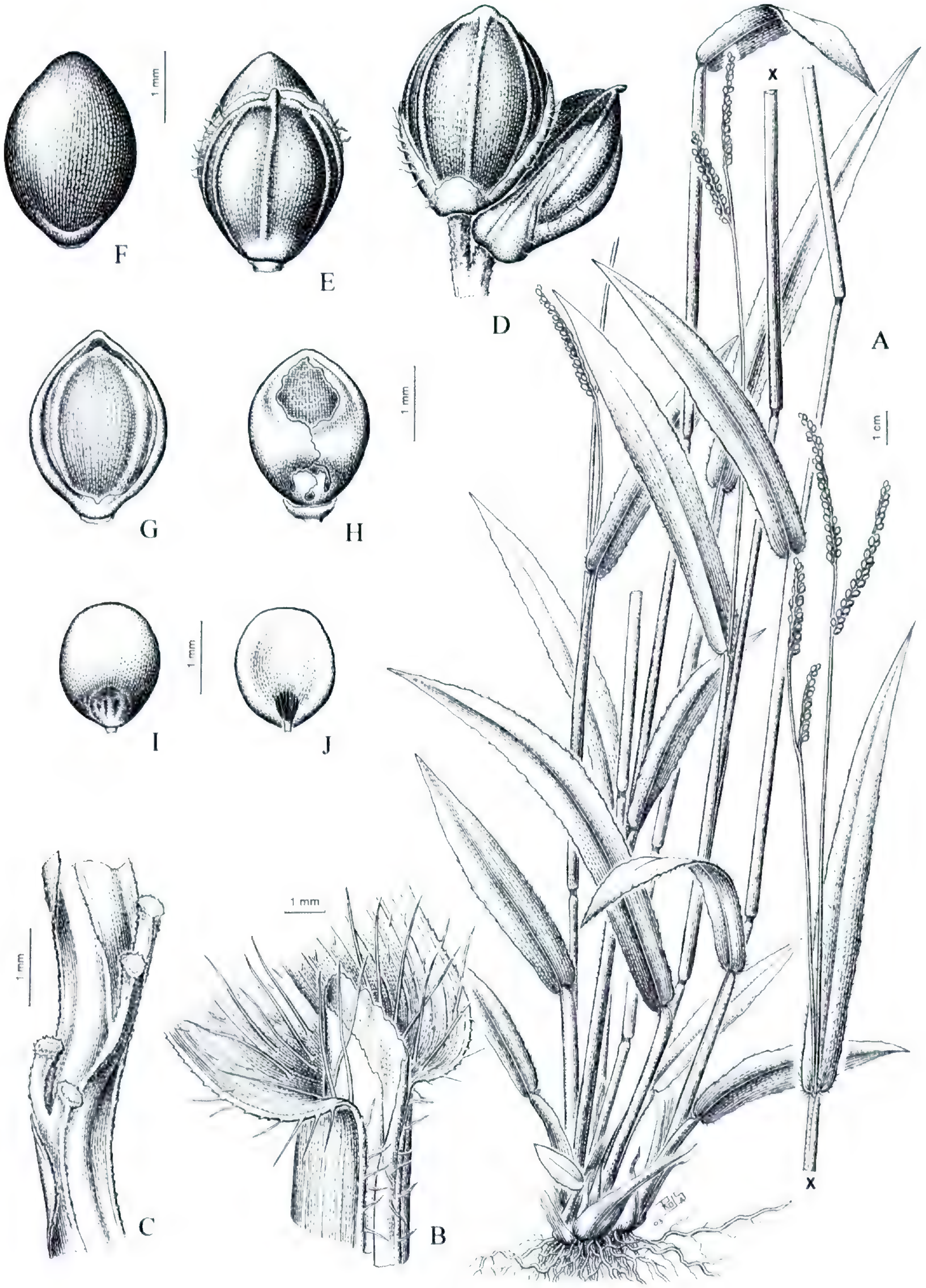

Figura 7. *Paspalum adoperiens.* —A. Hábito. —B. Detalle de la lígula. —C. Porción del raquis de los racimos, pedicelos. —D. Par de espiguillas, mostrando la gluma inferior dimorfa. —E. Espiguilla, vista dorsal mostrando la gluma superior. —F. Antecio superior, vista dorsal mostrando la lemma. —G. Antecio superior, vista ventral mostrando la pálea superior. —H. Pálea superior y lodículas. —I. Cariopsis, mostrando el embrión. —J. Cariopsis, mostrando el hilo. (A–J, *Hitchcock 9097.*)

de 2–2.7 mm de largo, (1.5–)1.7–1.9 mm de ancho, plano-convexas, pajizas o con tintes purpúreos, glabras o cilioladas en la gluma superior; *gluma inferior* dimorfa: de base ancha y de ápice obtuso, hasta 1/4 del largo de la espiguilla, centrada, glabra o en ocasiones ciliolada, enervia, en la espiguilla superior del par; ancha y de ápice obtuso o lanceolada y de ápice agudo a acuminado, 1/6–1/2 del largo de la espiguilla, centrada o excéntrica, glabra, en ocasiones ciliolada, 0–1-nervia en la espiguilla inferior del par; en ocasiones la gluma inferior es ausente en la mayor parte de las espiguillas de un racimo; *gluma superior* más corta que la espiguilla dejando libre el dorso apical del antecio superior, no papilosa, ciliolada en los márgenes y glabra o delicadamente pilosa en la superficie, en ocasiones completamente glabra, con el margen hialino, mucronada, 5-nervia, con los nervios marcados, con un nervio central y los restantes marginales, próximos entre sí; *lemma inferior* tan larga como la espiguilla, no sulcada, no papilosa, glabra, 5-nervia, con los nervios marcados, con un nervio central y los restantes marginales, próximos entre sí, con los márgenes doblados sobre el antecio; *pálea inferior* ausente o presente, cuando presente más corta o subigual a la lemma inferior, los nervios no endurecidos; *flor inferior* ausente; *antecio superior* obovoide a suborbicular, de 2–2.6 mm de largo, 1.7–1.8 mm de ancho, ligeramente cóncavo-convexo, crustáceo, pajizo, lemma y pálea con células cuadradas, de paredes onduladas, con papilas verrugosas regularmente distribuidas, centradas en las células, con dos a cuatro verrugas cada una, pelos bicelulares hacia el ápice de lemma y pálea, con la célula apical el doble del largo que la basal; lodículas de 0.5 mm de largo; estambres 3, anteras de 1–1.3 mm de largo. *Cariopsis* suborbicular a obovoide, de 1.5 mm de largo, 1.1 mm de ancho; hilo subcircular, 1/4–1/3 del largo de la cariopsis; embrión 1/3–1/2 el largo de la cariopsis.

Número cromosómico. $2n = 40$ (Davidse & Pohl, 1972a).

Distribución y ecología. Habita en México y en Centro América hasta Nicaragua (Fig. 8). Se observa una disyunción en la distribución de esta especie entre el estado de Sinaloa, al norte de México y el resto del área habitada, al sur de ese pais y Centro América. Crece en bosques de pinos o en pastizales, a lo largo de ríos o arroyos y en laderas, sobre suelos arenosos, entre 240–1500 m s.m.

Observaciones. Esta especie se caracteriza por sus láminas herbáceas, glabras a pilosas, por la presencia de dos pequeñas aurículas en los pulvínulos, y las espiguillas suborbiculares, con la gluma superior ciliolada sobre los márgenes o en la superficie, en ocasiones completamente glabra. La gluma inferior es dimorfa, no obstante puede estar ausente o escasamente desarrollada.

Paspalum adoperiens, *P. nutans* y *P. decumbens* se asemejan por sus espiguillas anchas y plano-convexas. Sin embargo, en *P. nutans* las espiguillas son anchamente elipsoides a obovadas, de 1.6–2.1 mm de largo y 1.1–1.4 mm de ancho, con la gluma inferior generalmente ausente. En *P. decumbens* las espiguillas son obovoides, de 1.2–1.8 mm de largo y 1–1.1 mm de ancho, y los racimos son solitarios.

Chase (1929) distingue a *Paspalum culiacanum* de *P. adoperiens* por la pilosidad de las láminas y la forma de las espiguillas, si bien considera que *P. culiacanum* podría ser un ejemplar excepcional de *P. adoperiens* con follaje glabro y espiguillas más angostas (1.5 mm). Pohl y Davidse (1994) separan a ambas especies por las láminas glabras, la forma elíptico-obovadas de las espiguillas, y por la gluma superior escasamente más corta que la espiguilla en *P. culiacanum*. Esta última especie es conocida sólo por el material tipo, procedente de Sinaloa, México; éste consiste en plantas con láminas glabras, con 3–5 racimos, espiguillas anchamente elipsoides, de (2–)2.3–2.5 mm de largo y 1.5–1.6 mm de ancho y la gluma inferior desarrollada sólo en algunas espiguillas. Del análisis del material de herbario puede concluirse que *P. adoperiens* presenta láminas y vainas glabras a pilosas, espiguillas suborbiculares, de 1.7–1.9 mm de ancho y la gluma inferior en ocasiones ausente. Así, por ejemplo, el ejemplar *Pohl & Gabel 13642* tiene hojas y vainas glabras pero las espiguillas tienen la forma suborbicular típica de la especie, y en el ejemplar *Morton & Makrinius 2559* se ha observado la gluma inferior de manera ocasional. Si bien *P. culiacanum* presenta una distribución disyunta con respecto a las poblaciones de *P. adoperiens*, se considera que no existe diferenciación morfológica suficiente para considear a este taxón como especie válida y se la incluye en la sinonimia de *P. adoperiens*.

Material representativo estudiado. EL SALVADOR. **La Paz:** along road ca. 1 km W of San Miguel Tepozontes, S of Lago Ilopongo, *Pohl & Gabel 13642* (MO). **San Salvador:** sin localidad, *Standley 23596* (US). **Santa Ana:** 13 km E of Metapán, *Pohl 12586* (MO). GUATEMALA. **Baja Verapaz:** along Hwy. CA-14 between El Progreso and Cobán, *Croat & Hannon 63676* (MO). **Guatemala:** between San Andrés y Muluá, *Weatherwax 218* (US). **Retalhuleu:** vicinity of Retalhuleu, *Standley 88678* (US). HONDURAS. **Francisco Morazán:** vicinity of El Zamorano, *Swallen 11002* (US); 16 km NW de El Zamorano, *Martínez et al. 12594*** (MEXU). **Olancho:** Mun. Jano, 16 mi. NE of La Unión along the road to Olanchito, *Davidse et al. 35480* (MO). **Santa Bárbara:** Trinidad, Finca Las Colmenas, *Salguero 4* (MO). MÉXICO. **Chiapas:** Re-

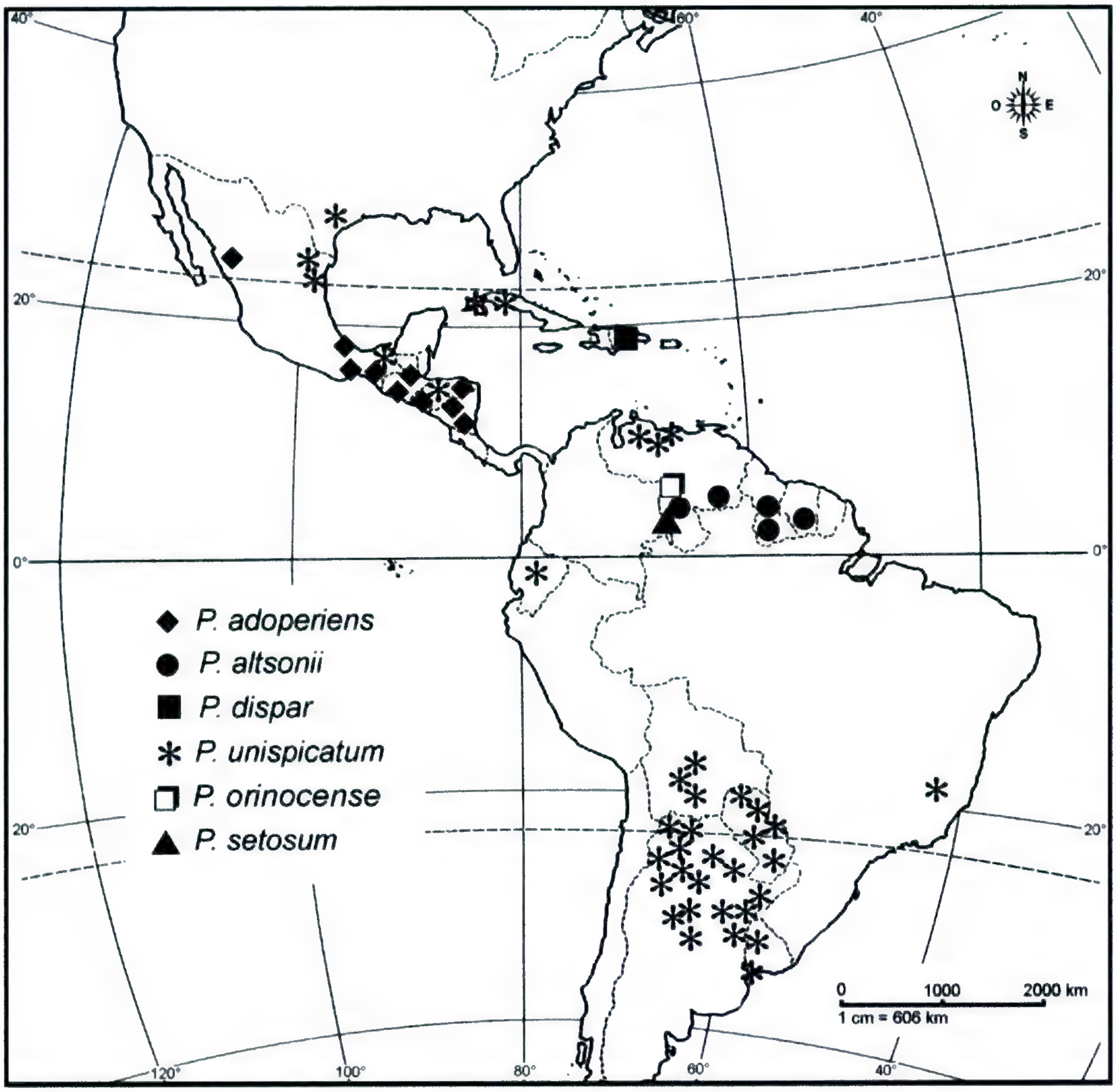

Figura 8. Distribución de *Paspalum adoperiens, P. altsonii, P. dispar, P. unispicatum, P. orinocense* y *P. setosum.*

serva El Triunfo, Mapastepec, *Heath & Long 1118* (MEXU). **Oaxaca:** vic. of Cafetal Concordia, *Morton & Makrinius 2559* (US). **Veracruz:** Zacualpan, *Purpus 8026** (US). NICARAGUA. **Matagalpa:** road betw. La Danta and La Luna, E of Esquiplas, *Stevens 11806* (MO). **Nueva Segovia:** N of Ocotal, *Seymour 5137* (MO).

3. Paspalum altsonii Chase, J. Washington Acad. Sci. 27(4): 144. 1937. TIPO: Guyana. Mazaruni Distr., 3 Sep. 1925, *R. A. Altson 392* (holotipo, US-1539437!, foto SI!; isotipos, K, MO-3326808). Figura 9.

Paspalum lucidulum Swallen, Bull. Torrey Bot. Club 75: 84. 1948. TIPO: Surinam. Tafelberg, *B. Maguire 24492* (holotipo, NY no visto; isotipos, K no visto, MO-1312732!, US-220936!, foto SI!, VEN-24492 no visto).

Plantas perennes, cespitosas, con rizomas de entrenudos cortos; *cañas* de 25–50 cm de alto, 2–3 mm de ancho, erectas a decumbentes, ramificadas en los nudos inferiores; entrenudos de 3–12 cm de largo, comprimidos, glabros; nudos glabros, castaños. *Vainas* de 3–9 cm de largo, las basales flojas, glabras o pilosas, los márgenes hialinos, pestañosos en toda su longitud o hacia el ápice; *lígulas* membranáceas, de 1.5–3 mm de largo, castañas; seudolígula ausente o presente, cuando presente, con pelos de 1.5–2 mm de largo; cuello glabro a piloso; *láminas* linear-lanceoladas, de 5–15(–21) cm de largo, 0.5–1.2 mm de ancho, planas, aquilladas, herbáceas, de base redondeada o atenuada, ápice acuminado, glabras a pilosas en ambas caras, los márgenes escabrosos y pilosos. *Pedúnculos* 1–4 en la última vaina foliar, exertos a subincluidos, hasta de 20 cm de largo, filiformes, pilosos a esparcidamente pilosos, raro glabros; frecuentes en vainas subapicales y medias. *Inflorescencias* terminales y

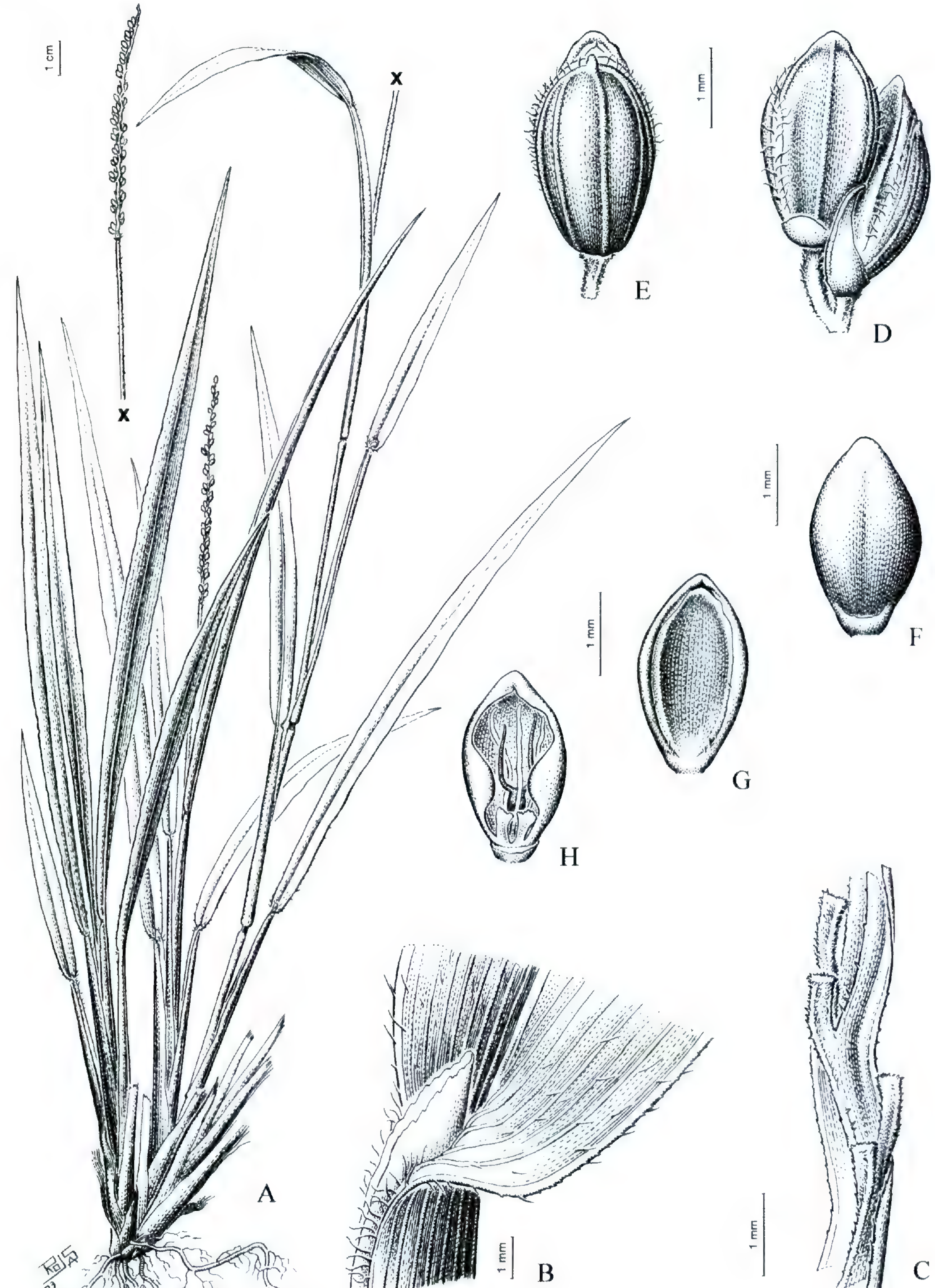

Figura 9. *Paspalum altsonii.* —A. Hábito. —B. Detalle de la lígula. —C. Porción del raquis de los racimos, pedicelos. —D. Par de espiguillas, mostrando la gluma inferior dimorfa. —E. Espiguilla, vista dorsal mostrando la gluma superior. —F. Antecio superior, vista dorsal mostrando la lemma. —G. Antecio superior, vista ventral mostrando la pálea. —H. Pálea superior, lodículas y gineceo. (A–H, *Davidse & Miller 27022.*)

axilares; racimos 1, raro 2, arqueados; eje principal ausente o de 1–2 cm de largo, piloso; pulvínulos pilosos; raquis de los racimos de 3–6(–8) cm de largo, 0.4–0.9 mm de ancho, con cortas extensiones laterales a triquetro, acanalado, glabro en la cara adaxial e hispídulo en la cara abaxial o ambas caras pilosas, márgenes glabros, terminando en una espiguilla desarrollada; pedicelos en pares, desiguales, breves, el de la espiguilla superior hasta de 1 mm de largo, glabros a esparcidamente pilosos; espiguillas imbricadas, irregularmente dispuestas en 4 series. *Espiguillas* elipsoides, de 2–2.8(–3) mm de largo, 1.2–1.4 mm de ancho, cóncavo convexas a plano-convexas, pajizas a verdosas, esparcidamente pubescentes, raro glabras; *gluma inferior* dimorfa: ancha y con el ápice obtuso o bilobulado, hasta 1/6 del largo de la espiguilla, glabra o con unos pocos pelos en la base, excéntrica, enervia, en la espiguilla superior del par; lanceolada, triangular o bilobulada, 1/5–1/2 del largo de la espiguilla, glabra o con unos pocos pelos en la base o en la superficie, excéntrica, enervia o 1-nervia en la espiguilla inferior del par; *gluma superior* ligeramente más corta que la espiguilla, papirácea, no papilosa, ciliolada en los márgenes basales y medios, o junto al ápice, con pelos delgados, hasta de 0.5 mm de largo, raro completamente glabra, 5-nervia, con un nervio central, los restantes marginales, próximos entre sí; *lemma inferior* tan larga como la espiguilla, en ocasiones sobrepasando ligeramente el ápice del antecio, cartácea, con el dorso suavemente sulcado, finamente papiloso o liso, glabra en la superficie y glabra a escasamente pilosa en los márgenes, 5-nervia, con un nervio central, los restantes marginales, próximos entre sí, marcados, con los márgenes doblados sobre el antecio; *pálea inferior* tan larga como su correspondiente lemma o levemente menor, hialina; *flor inferior* ausente; *antecio superior* elipsoide, 1.5–2.2 mm de largo, 1–1.2 mm de ancho, plano-convexo a ligeramente cóncavo-convexo, crustáceo, pajizo, fuertemente papiloso, lemma y pálea con células cuadradas, de paredes onduladas, con papilas verrugosas distribuidas regularmente, centradas en las células, con 4–6 verrugas, cada una, escasos pelos bicelulares hacia el ápice de la pálea; lodículas de 0.3 mm de largo; estambres 3, anteras de 0.8–1 mm de largo. *Cariopsis* anchamente elipsoide, de 1.3 mm de largo, 1 mm de ancho; hilo elíptico, 1/3 del largo de la cariopsis; embrión 1/3 del largo de la cariopsis.

Distribución y ecología. *Paspalum altsonii* crece en Venezuela, en los estados de Amazonas y Bolívar, en Guyana y en Surinam, en bosques, sobre suelos arenosos o rocosos o en márgenes de cursos de agua, entre los 130–1200 m s.m. (Fig. 8).

Observaciones. Esta especie se caracteriza por presentar 1–4 pedúnculos, usualmente pilosos, con 1, raro 2 racimos, de 3–6(–8) cm de largo y espiguilla con la gluma superior pilosa en los márgenes o junto al ápice, con pelos cortos y delgados, ocasionalmente las espiguillas son completamente glabras. El ápice de la gluma inferior es obtuso o bilobulado en la espiguilla superior y lanceolado, triangular o bilobulado en la superior.

El ejemplar *Davidse & Miller 27022* presenta pedúnculos glabros, láminas hasta de 21 cm de largo y espiguillas de 2.8–3 mm de largo. En el espécimen *Jansen-Jacobs et al. 690* se observan glumas glabras en la mayoría de las espiguillas, con sólo algunas espiguillas delicadamente pilosas en sus racimos; mientras que *Jansen-Jacobs et al. 1231* presenta espiguillas con unos pocos pelos en la gluma superior y el raquis de los racimos densamente piloso en la cara abaxial y piloso en la adaxial.

Paspalum altsonii es afín a *P. nutans* y a *P. pilosum*. De *P. nutans* se separa porque en esta especie la gluma inferior está desarrollada ocasionalmente en algunas de las espiguillas de un racimo, las espiguillas son glabras (a veces cilioladas en la gluma superior) y anchamente elipsoides a obovoides. *Paspalum pilosum* y *P. altsonii* poseen espiguillas similares, con la lemma inferior papilosa y sulcada longitudinalmente; se diferencian porque *P. pilosum* tiene espiguillas glabras y las plantas son de mayor porte, con cañas de 40–100 cm de alto (vs. 25–50 cm), láminas de 10–40 cm de largo [vs. 5–15(–21) cm], racimos más largos [4–15(–20) cm vs. 3–6(–8) cm] y raquis más ancho (0.8–1.5 mm vs. 0.4–0.9 mm).

La presencia de ejemplares con las espiguillas glabras o escasamente pilosas en *Paspalum altsonii*, sumado al tamaño de las plantas, que representa el extremo inferior de las medidas halladas en *P. pilosum*, podría sugerir que ambas entidades representan una misma especie. En el presente tratamiento se las mantiene como especies separadas hasta tanto se coleccionen más ejemplares de *P. altsonii*.

Material representativo estudiado. GUYANA. Kaieteur savanna, *Sandwith 1381*/***(US); Kanuku, *Jansen-Jacobs et al. 1231* (US); Kanuku, Nappi-haed, *Jansen-Jacobs et al. 690* (US). SURINAM. 9 km N of Lucie River and 12 Km W of Oost river, 3°36′N, 56°30′W, *Maguire et al. 54234* (US). VENEZUELA. **Amazonas:** Rio Negro, betw. Neblina and Canyon Grande, *Davidse & Miller 27022* (SI, US). **Bolívar:** Piedra de la Virgen, *Morrone et al. 4798* (SI).

4. Paspalum auricomum (A. G. Burm.) S. Denham, comb. nov. Basónimo: *Thrasya auricoma* A. G. Burm., Brittonia 34: 461. 1982. TIPO: Brasil. Pará: Serra do Cachimbo, 425 m, 14 Dec. 1956, *J. Pires, G. A. Black, J. J. Wurdack & N. T. Silva 6229* (holotipo, IAN no visto; isotipo, US no visto).

Referencias. Para descripción e ilustración de esta especie véanse protólogo y Burman (1985 [1987]).

Distribución y ecología. Especie endémica de la Sierra de Cachimbo, al sur del estado de Pará, Brasil (Fig. 6); crece sobre suelos arenosos o pedregosos.

Observaciones. Es característico de esta especie el raquis foliáceo y densamente piloso en los márgenes y la superficie adaxial, con pelos papilosos, dorados y patentes a la superficie del raquis; presenta matas densas, hasta de 40 cm de alto, las láminas son lineares, de 0.1 cm de ancho y las espiguillas pilosas, sin la gluma inferior y con la gluma superior 2-nervia (Burman, 1982, 1985 [1987]).

Material estudiado. BRASIL. **Pará:** Itaituba, Cachimbo, *Silva et al. 92*/*** (MO, US).

5. Paspalum axillare Swallen, Bull. Torrey Bot. Club 75: 84. 1948. *Thrasya axillaris* (Swallen) A. G. Burm. ex Judz., Fl. Guianas, ser. A, Phanerog. 8(187): 630. 1990. TIPO: Surinam. Tafelberg, 10 Sep. 1944, *B. Maguire 24678* (holotipo, US!, foto SI!; isotipo, US no visto).

Paspalum ramianum Camacho Rodr.-Rodr. & L. Guevara, Ernstia 8: 105. 1999. TIPO: Venezuela. Bolívar: Distrito Piar, Guayaraca, 25–27 Nov. 1982, *G. Davidse & O. Huber 22665* (holotipo, VEN no visto).

Referencias. Para descripción e ilustración de esta especie véase protólogo.

Distribución y ecología. Judziewicz (1990) cita ejemplares de esta especie coleccionados en Brasil (Amazonas), Venezuela (Bolívar) y en Surinam (Fig. 10); crece cerca de cuerpos de agua o en laderas húmedas.

Observaciones. Es una especie anual, con matas de 20–40 cm de alto, con racimos de hasta 3 cm de largo y espiguillas delicadas y pequeñas (0.9–1.1 mm de largo, 0.5 mm de ancho), con un callo en la base; la gluma inferior es ausente y la superior es de 1/2 del largo de la espiguilla y enervia. El antecio presenta papilas simples.

Material estudiado. VENEZUELA. **Amazonas:** Río Negro, Aracamuni, *Liesner & Delascio 22186*/*** (SI, US).

6. Paspalum botterii (E. Fourn.) Chase, J. Washington Acad. Sci. 13(20): 436. 1923. *Dimorphostachys botterii* E. Fourn., Mexic. Pl. 2: 14. 1886. TIPO: México. Veracruz: Orizaba, *M. Botteri 118* (holotipo, P!; isotipo, US-865864!).

Dimorphostachys paspaloides E. Fourn., Mexic. Pl. 2: 14. 1886. TIPO: México. Veracruz: *Gouin 32* (lectotipo, designado por Chase (Contr. U.S. Natl. Herb. 28: 110. 1929), P!; isotipo, US-865863!).

Dimorphostachys langei E. Fourn., Mexic. Pl. 2: 14. 1886. Syn. nov. *Paspalum langei* (E. Fourn.) Nash, N. Amer. Fl. 17: 179. 1912. TIPO: México. Mecapalco, *F. M. Liebmann 179*, en parte (lectotipo, designado por Chase (Contr. U.S. Natl. Herb. 28: 105. 1929), C no visto; isotipo, US-80067!).

Paspalum lineare E. Fourn., Mexic. Pl. 2: 12. 1886, non *Paspalum lineare* Trin., Gram. Panic. 99. 1826. TIPO: México. *F. M. Liebmann 192* (lectotipo, designado por Chase (Contr. U.S. Natl. Herb. 28: 104. 1929), C no visto; isotipo, US-80067!).

Dimorphostachys drummondii E. Fourn., Mexic. Pl. 2: 15. 1886. *Paspalum drummondii* (E. Fourn.) Vasey, Contr. U.S. Natl. Herb. 3(1): 18. 1892, non *Paspalum drummondii* Müll. Hall., Bot. Zeitung (Berlin) 19: 332. 1861. TIPO: E.U.A. Texas: *J. Drummond 350* (lectotipo, designado por Chase (Contr. U.S. Natl. Herb. 28(1): 105. 1929), P no visto; isotipo, US-865866!, foto SI!).

Paspalum abbreviatum Trin. ex E. Fourn., Mexic. Pl. 2: 10. 1886. TIPO: México. Veracruz: *C. J. W. Schiede 888* (holotipo, LE no visto; isotipo, US-951532 no visto).

Panicum squamatum E. Fourn., Mexic. Pl. 2: 18. 1886. TIPO: País no indicado, Nuevo Mundo, *W. F. Karwinski 982* (holotipo, LE no visto; isotipo, US-951571!).

Dimorphostachys ciliifera Nash, Fl. S.E. U.S. 78: 1327. 1903. *Paspalum ciliiferum* (Nash) Hitchc., Contr. U.S. Natl. Herb. 12(6): 201. 1909. TIPO: E.U.A. Florida: *J. H. Simpson 97* (holotipo, US-2854668!).

Paspalum palmeri Chase, Contr. U.S. Natl. Herb. 28(1): 109. 1929. Syn nov. Nombre reemplazado: *Paspalum setaceum* Michx. var. *pubiflorum* Vasey, Contr. U.S. Natl. Herb. 1: 114. 1891. TIPO: México. Sonora: *E. Palmer 704* (holotipo, US-951577!; isotipos, W!, US-824351!, US-824352!, US-1060374!).

Plantas perennes, cespitosas; rizomas de entrenudos cortos, *cañas* de 30–140 cm de alto, 1–4 mm de diámetro, erectas a decumbentes, esparcidamente ramificadas; entrenudos de 5–20 cm de largo, cilíndricos a ligeramente comprimidos, estriados, glabros; nudos glabros a pilosos. *Vainas* de 5–17 cm de largo, usualmente más cortas que los entrenudos, aquilladas, papiloso-pilosas, los márgenes glabros a pestañosos; *lígulas* membranáceas, de 1–1.5 mm de largo, castañas; seudolígula formada por un mechón de pelos hasta de 7 mm de largo; cuello piloso; *láminas* linear-lanceoladas, de 7–40 cm de largo, 0.6–2(–2.4) cm de ancho, planas, de base atenuada a subcordada y ápice agudo a acuminado, cortamente pilosas a papiloso-pilosas

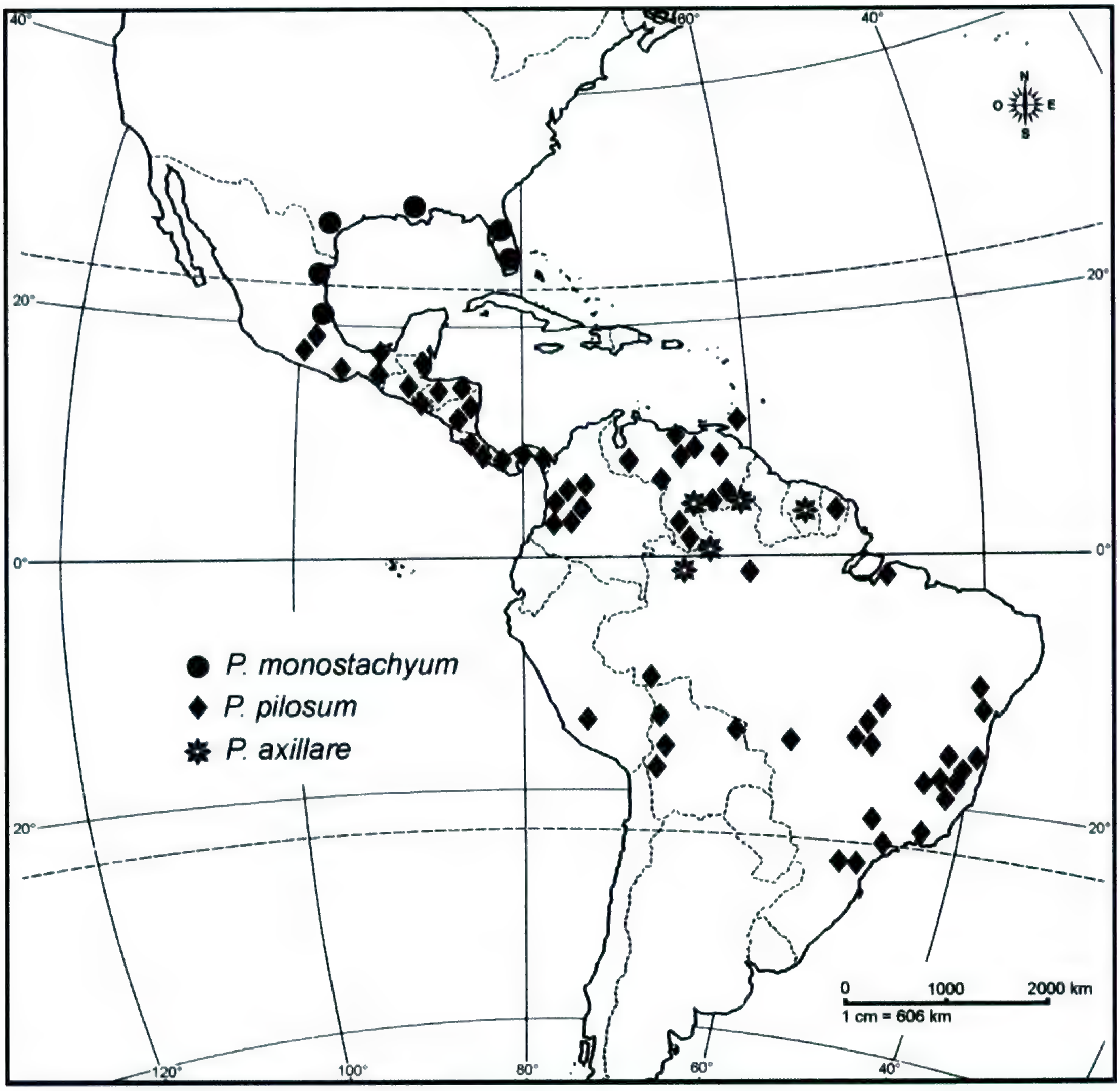

Figura 10. Distribución de *Paspalum monostachyum, P. pilosum* y *P. axillare.*

en ambas caras, los márgenes escabrosos, glabros a pestañosos. *Pedúnculos* 1(3) en la última vaina foliar, exertos o subincluidos, hasta de 40 cm de largo, glabros; comúnmente con pedúnculos incluidos en las vainas inferiores o medias. *Inflorescencias* terminales y axilares; racimos 1–9(16), arqueados, divergentes, solitarios o alternos; eje principal ausente o de 5–15 cm de largo, aplanado, glabro; pulvínulos pilosos, con pelos hasta de 7 mm de largo; raquis de los racimos de 3–18 cm de largo, 0.9–1.1 mm de ancho, con cortas extensiones laterales, los márgenes glabros a esparcidamente pilosos, terminando en una espiguilla desarrollada; pedicelos en pares, subiguales a desiguales, el de la espiguilla superior hasta de 2 mm de largo, escabrosos; espiguillas irregularmente distribuidas en 2–4 series. *Espiguillas* elipsoides a ligeramente obovoides, de 2–3 mm de largo, 1.2–1.4 mm de ancho, plano-convexas, pubescentes, con pelos cortos hasta de 0.3 mm de largo, delgados, pálidas a ferrugíneas, maculadas o con manchas glandulares; *gluma inferior* dimorfa: ausente o presente en la espiguilla superior del par, cuando presente vestigial, menor a 1/6 del largo de la espiguilla o ancha y de ápice obtuso a agudo, hasta de 1/3 de la espiguilla, centrada, los márgenes ciliados, enervia o 1-nervia; ausente o presente en la espiguilla inferior del par, cuando presente ancha, de ápice obtuso y de 1/6 del largo de la espiguilla, o bien lanceolada u ovada, hasta 3/4 del largo de la espiguilla, excéntrica, esparcidamente pilosa en la superficie y 1-nervia; *gluma superior* ligeramente más corta o tan larga como la espiguilla, abrazando a la lemma inferior desde la base hasta 1/3–1/2 de su longitud, no papilosa, cortamente pubescente, con pelos adpresos regularmente distribuidos, 3–5-

nervia, con un nervio medio, los restantes marginales, próximos entre sí; *lemma inferior* tan larga como la espiguilla, no papilosa, no sulcada, membranácea a papirácea, glabra a esparcidamente pubescente, con los márgenes doblados sobre el antecio y abrazándolo, 3–5-nervia, con un nervio central y los restantes marginales, próximos entre sí; *pálea inferior* ausente o reducida; *flor inferior* ausente; *antecio superior* anchamente elipsoide, 2–2.5 mm de largo, 1.2–1.3 mm de ancho, planoconvexo, crustáceo, pajizo a ferrugíneo, lemma y pálea con células cuadradas, de paredes onduladas, con papilas verrugosas distribuidas regularmente, centradas en las células, con 2–5 verrugas en cada célula, micropelos bicelulares dispersos en el ápice de lemma y pálea, con la célula apical 1.5 más larga que la basal; lodículas de 0.2–0.3 mm de largo; estambres 3, anteras de 0.8–1 mm de largo. *Cariopsis* elipsoide a obovoide, de 1.2–1.7 mm de largo, 0.9–1.5 mm de ancho; hilo anchamente elíptico, 1/3 del largo de la cariopsis; embrión 1/4–1/3 del largo de la cariopsis.

Iconografía. R. W. Pohl, Flora Costaricensis: 406, fig. 147. 1980.

Nombres vulgares. "camalote" (*Galván et al. 477*), "zacate" (*Chavelas & Perez 16, Martinez & Calderón 130*), "trensilla," "bahía" (Beetle et al., 1999).

Número cromosómico. $n = 40$ (Davidse & Pohl, 1978), $2n = 40$, $2n = 60$ (Burton, 1942), $2n = 80$ (Reeder, 1967).

Distribución y ecología. Habita desde los Estados Unidos de América (en los estados de Texas y Florida), en México y Mesoamérica, hasta Venezuela y Colombia; también en el Caribe, en Cuba y Haití. Swallen (1955) cita a *Paspalum langei* para Louisiana, Estados Unidos de América (Fig. 11). Crece en llanos o pendientes de bosques tropicales, caducifolios a subperennifolios, en bordes de caminos y en cultivos (café, maíz, mango); sobre suelos arcillosos, de piedra caliza o suelos inundables; desde el nivel del mar a los 2000 m s.m. Especie forrajera (Mejía Saulés & Dávila Aranda, 1992).

Observaciones. Esta especie se caracteriza por sus espiguillas elipsoides a ligeramente obovoides, pubescentes, maculadas o con manchas glandulares. La presencia de la gluma inferior es variable, desde ausente o breve en ambas espiguillas, reducida o ausente en la espiguilla superior y desarrollada en la inferior o desarrollada en ambas espiguillas. Además, la distribución de la gluma inferior puede variar a lo largo de un mismo racimo.

Paspalum botterii se asemeja a *P. variabile, P. subfalcatum* y *P. inconstans* por presentar espiguillas pilosas. Las diferencias entre ellas se discuten en cada una de las tres últimas especies.

Fournier (1886) al describir a *Paspalum macrophyllum* Kunth var. *piliferum* cita tres sintipos coleccionados en México: *Botteri 117*, de Orizaba, *Liebmann 167* (mal nombrado 117), de Consoquitla y *Liebmann 168*, de Santa María Tlatella; de los cuales este último es seleccionado como lectotipo (P!) por coincidir con el protólogo de la especie. Estos tres ejemplares llevan el nombre *Paspalum varians* con letra de Fournier, este nombre es un nomen nudum ya que Fournier (1886) lo cita sin descripción al compararlo con *Paspalum abbreviatum*.

El holotipo de *Panicum squamatum* (*Karwinski 982*) no fue localizado; sin embargo, Chase (1929) cita un ejemplar en LE. Por otra parte, *Karwinski 982* fue citado por Fournier (1886) también como sintipo de *Dimorphostachys drummondi*, especie que Chase (1929) lectotipifica con el ejemplar *Drummond 350*.

Chase (1929) relaciona a *Paspalum palmeri* con *P. botterii* por el tipo de distribución de la gluma inferior, pero separa a ambas especies por el número de racimos (1–3 en *P. palmeri* vs. 4–15 en *P. botterii*) y por el ancho de las láminas (menores a 1 cm en *P. palmeri* vs. 1–2.4 cm en *P. botterii*). La autora menciona que las espiguillas del ejemplar tipo, *Palmer 704*, son inmaduras y que probablemente a la madurez se tornen parduscas y con manchas glandulares. Beetle et al. (1999) distingue a *P. palmeri* por el largo de sus espiguillas (2.8–3.2 mm vs. 2–2.6 mm en *P. botterii*) y por el número de racimos [1–3 vs. (3)4–5 en *P. botterii*]. McVaugh (1983) relaciona a *P. botterii* y *P. palmeri* por su aspecto, pero las separa por los racimos y espiguillas más largas en *P. palmeri* [racimos de (3.5–)8–4 cm vs. (4–)6–10(–14) cm y espiguillas de 2.8–3.2 mm vs. 2.3–2.6 mm]. El análisis de los ejemplares tipo y de abundante material de herbario permite concluir que existe una gradación continua en los caracteres anteriormente señalados, por lo que en el presente estudio se incluye a *P. palmeri* en la sinonimia de *P. botterii*.

El carácter más ampliamente usado para separar a *Paspalum botterii* de *P. langei* ha sido la distribución de la gluma inferior en el par de espiguillas. Fournier (1886) separa a las especies de *Dimorphostachys* en dos grupos de acuerdo a la ausencia (grupo 1, con *D. botterii*) o presencia (grupo 2, con *D. langei*) de la gluma inferior en la espiguilla superior del par. Chase (1929) distingue a *P. langei* de *P. botterii* por presentar la primer especie espiguillas con manchas glandulares y la gluma in-

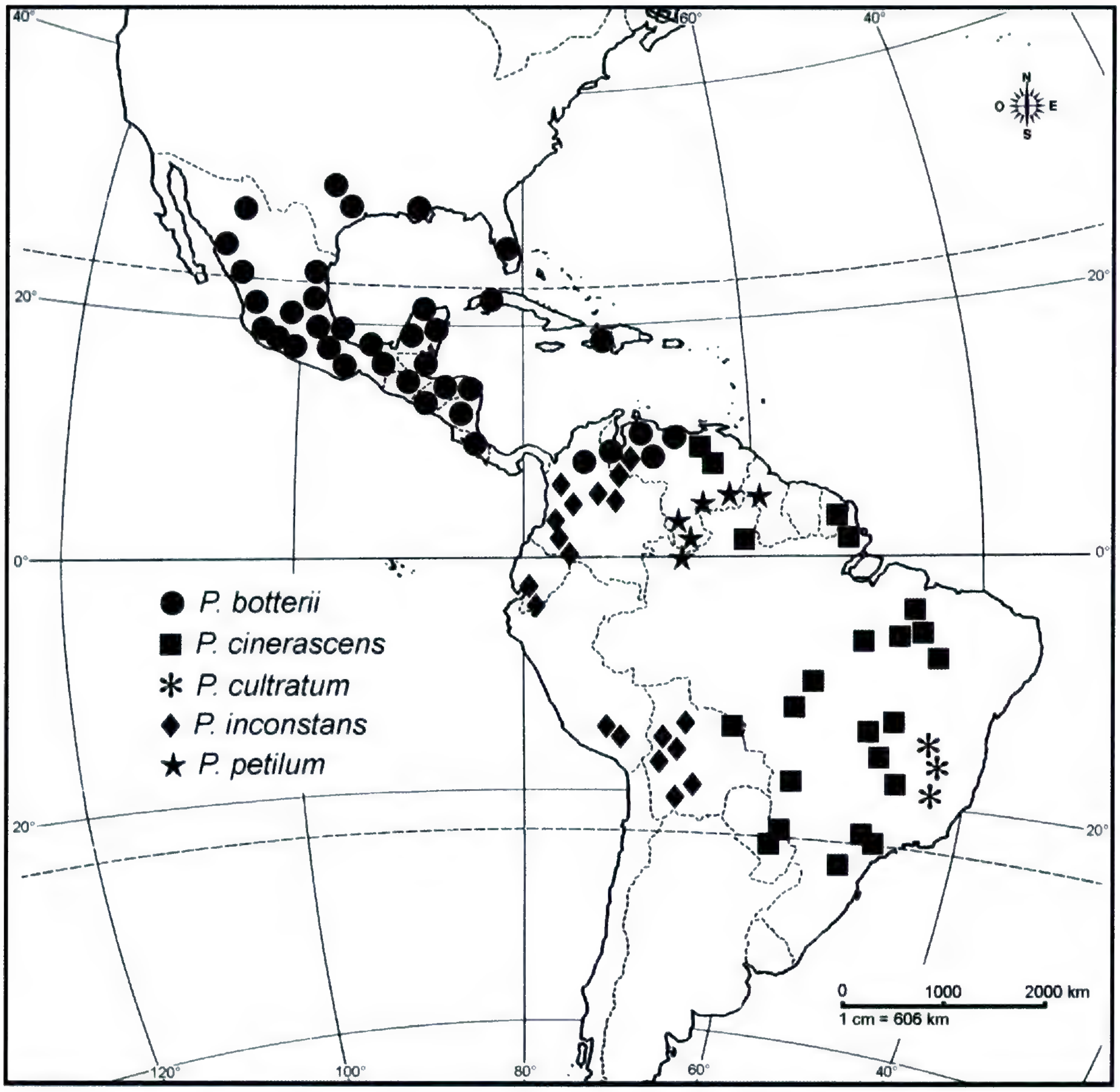

Figura 11. Distribución de *Paspalum botterii, P. cinerascens, P. cultratum, P. inconstans* y *P. petilum.*

ferior en ambas espiguillas del par, raro ausente en la espiguilla superior, mientras que *P. botterii* presenta la gluma inferior obsoleta o inconspicua en la espiguilla superior y comúnmente obsoleta en la espiguilla inferior. Luego, en la descripción de *P. botterii*, la autora se contradice al describir a la gluma inferior como obsoleta en la espiguilla primaria y comúnmente desarrollada en la mayoría de las espiguillas secundarias y señala que en algunos ejemplares alcanza 1/2 del largo de la espiguilla. Esta característica se observa en la lámina publicada en ese trabajo, basada en *Botteri 118*, ejemplar tipo, y en *Botteri 659*. Por otra parte, Pohl (1980), McVaugh (1983) y Pohl y Davidse (1994), coinciden al describir que, en *P. botterii*, la gluma inferior de la espiguilla superior del par es ausente, mientras que está ausente o presente en la espiguilla inferior. Con respecto a los caracteres vegetativos, Chase (1929) describe a *P. botterii* como plantas robustas, de 60–130 cm de alto, con láminas comúnmente de más de 20 cm y hasta 2.4 cm de ancho. En las observaciones de *P. langei* destaca ciertos ejemplares coleccionados por *Hitchcock* (*8630, 8681, 8686* y *8744*) como plantas robustas, similares a *P. botterii*.

El estudio del material tipo de ambas especies y de un elevado número de ejemplares reveló una amplia variabilidad en la distribución de la gluma inferior y una continuidad en los caracteres vegetativos. La variabilidad en la distribución de la gluma inferior puede hallarse en distintos ejemplares o a lo largo de un mismo racimo de un ejemplar determinado. Así, en los ejemplares *Reeder & Reeder 4434, Davidse et al. 20421, Reeder & Reeder 3007* y *Miranda 1057*, la gluma inferior varía desde ausente, poco desarrollada o hasta 2/3 del largo de

la espiguilla, en diferentes espiguillas de un mismo racimo. La gluma inferior puede estar presente en ambas espiguillas, pero de mayor longitud en la espiguilla basal del par (en *Chavelas & Perez 13*), puede estar ausente en la espiguilla superior y presente en la inferior (en *Hitchcock 8956* y *Reeder & Reeder 4301*), puede ser ausente o reducida en ambas espiguillas del par (en *Santana 2970*), o la gluma inferior puede estar totalmente ausente, excepto en unas pocas espiguillas inferiores (en *Pringle 3779*). La gluma inferior puede ser isomorfa en las espiguillas de un par (en *Davidse et al. 20293* y *Burandt V0159*, 0.4–1 mm de largo) o la gluma inferior sólo puede estar presente en las espiguillas apicales del racimo (*Guzmán & Cuevas 1082*). En relación al porte de las plantas, es frecuente la presencia de plantas robustas con espiguillas ligeramente obovoides, y la gluma inferior sólo presente en la espiguilla inferior del par. Pero se observaron plantas robustas, tales como *Macías 3527* y *Pascual & Martínez 471*, de 110–140 cm de alto, con láminas de 23–40 cm de largo y 1–2 cm de ancho, con espiguillas elipsoides y gluma inferior presente en ambas espiguillas del par. A su vez, son frecuentes las plantas no robustas, con espiguillas elipsoides, y gluma inferior presente en ambas espiguillas del par; sin embargo, los ejemplares *Santana & Lorente 3728* y *Spellenberg et al. 12207* son plantas delicadas, de 38–65 cm de alto, con láminas de 8–17 cm de largo y 0.6–0.7 cm de ancho, con espiguillas dispuestas no imbricadas sobre los racimos y con la gluma inferior sólo presente en las espiguillas inferiores del par. Finalmente, la presencia de manchas glandulares en la gluma superior y lemma inferior no es exclusivo de especímenes con gluma inferior presente en ambas espiguillas; así, *Hinton 4515*, con la gluma inferior ausente en la espiguilla superior y ocasionalmente presente en la inferior del par, presenta la gluma superior y lemma inferior con manchas glandulares en la base. Consecuentemente, no pueden establecerse caracteres diagnósticos para ambas entidades y se considera a *P. langei* como sinónimo de *P. botterii*.

Material representativo estudiado. BELIZE. **Belize:** Gracie Rock, *Croat 23828* (MO). **Cayo:** along road betw. Millonario and Grano de Oro, *Croat 23700* (MO). **Toledo:** Machaca, *Gentle 6882* (US). COLOMBIA. **Bolívar:** near Turbaco, *Killip & Smith 14367* (US). COSTA RICA. **Guanacaste:** Santa Rosa Nat. Park, Playa Naranjo beach, *Liesner 4364* (MO). **Puntarenas:** Isla San Lucas, Golfo de Nicoya, *Grayum et al. 4256** (MO, SI). CUBA. **Habana:** Finca Santa Teresa, El Calvario, *Leon 934* (US). **Pinar del Río:** Mariel, Loma la Gobernadora, *Ekman 934* (SI). EL SALVADOR. **San Salvador:** *Hitchcock 8956* (SI, US). **Santa Ana:** Hda. San Jose, *Rohweder 2075* (MO). ESTADOS UNIDOS DE AMÉRICA. **Florida:** Orange Bend, *Chase 932* (MO). **Texas:** Brazoria Co., *Tharp 43157* (MO). GUATEMALA. **Alta Verapaz:** 5 km NO de Cobán, *Standley 12031* (US). **Guatemala:** Guatemala City, *Hitchcock 9079* (US). **Petén:** 2 mi. S of entrance of Tikal Nat. Park, *Croat 24702* (MO). HAITÍ. Sin loc.: *Ekman 5948* (US). HONDURAS. **Atlántida:** valley of Río Cangrejal, 17 km SSE of La Ceiba, *Pohl & Davidse 112085* (MO). **Colón:** Trujillo, Río Negro, SE del Cerro Capiro, *Clotter 11* (MO). **El Paraíso:** Río Choluteca, road to Yuscaran, *Swallen 10876* (US). **Islas de la Bahía:** Cayos de Utila, *Espinoza 160* (MO). **Francisco Morazán:** El Zamorano, *Standley 23785* (US). **Olancho:** faldas del Cerro El Boquerón, 20 km NE de Juticalpa, *Abraham Palma 30* (MEXU, MO). **Santa Bárbara:** 20 km NE of Nueva Arcadia, *Harmon & Dwyer 3804* (MO). MÉXICO. **Campeche:** Champotón, 120 km SO Xpujil, *Pascual & Martinez 471* (MEXU); 4 km W of Escárcega, *Davidse et al. 20293* (MEXU). **Chiapas:** Ocosingo, *Davidse et al. 20421* (MEXU). **Chihuahua:** Ocampo, *Spellenberg et al. 12207* (MEXU). **Colima:** 2 km SE Platanarillo, *Guzmán & Cuevas 1082* (MEXU). **Guerrero:** 15 mi. N of Tierra Colorada, *Reeder & Reeder 3007* (MEXU). **Hidalgo:** 6 km E de Tenango de Doria, *Hernandez 3372* (MEXU). **Jalisco:** Tonaya, *Santana 2970* (MEXU); 13 mi. S of Autlán, *Reeder & Reeder 4434* (US); Autlán, *Santana & Lorente 3728* (MEXU); El Limón, *Macías 3527* (MEXU). **México:** Temascalpetec, Piedra Grande, *Hinton 4515* (BAA). **Michoacán:** N of Jungapeo, *Sohns 691* (US). **Morelos:** Cuernavaca, *Hitchcock 6826* (US). **Nayarit:** 10 mi. SE of Ahuacatlán on the road to Barranca del Oro, *McVaugh & Koelz 820* (US). **Nuevo León:** 37 km SE of Monte Morelos, *Gould 12568* (MEXU). **Oaxaca:** km 14 carretera Tuxtepec–Pueblo Viejo, *Chavelas & Perez 13* (MEXU). **Puebla:** 10 mi. NE of Xicotepec, *Reeder & Reeder 4301* (MEXU); Jolalpan, 8 km NE de Huahuchinatla, *Miranda 1057* (MEXU). **Quintana Roo:** San José de la Montaña, 9 km S of Hwy. 186 km Hwy. to Thomas Garrido, *Davidse et al. 20273* (MO). **San Luis Potosí:** Las Canoas, *Pringle 3779* (MEXU). **Sinaloa:** Rancho del Burro, *Ortega 4102* (US). **Sonora:** Alamos, *Gentry 337* (US). **Tabasco:** Cárdenas, en la carretera Cárdenas–Huimanguillo, *Suarez 82* (MEXU). **Tamaulipas:** sin loc., *Wooton s.n.* (US). **Veracruz:** Zongolica, El Palmar, *Vera Santos 2300* (US). **Yucatán:** sin loc., *Lundell 951* (MEXU). NICARAGUA. **Boaco:** Boaco, *Seymour 3846* (MO). **Carazo**: Route 2, Santa Teresa, *Atwood 1272* (MO). **Estelí:** N slope of Cerro El Fraile, *Stevens & Montiel 18098* (MO). **Granada:** near Granada, Nt. Mombacho, *Grant 779* (US). **Jinotega:** sin loc., *Hitchcock 8724* (US). **Managua:** Rt. 1, Km 17, Tipitapa, *Seymour 3436* (MO). **Masaya:** Masaya, *Hitchcock 8630½* (US). **Matagalpa:** Matagalpa, *Zelaya 2304* (MO). **Nueva Segovia:** ca. 5.2 km N of San Fernando, valley of Río San Fernando, *Stevens 3294* (MO). **Rivas:** Isla de Ometepe, La Argentina, *Moreno 22115* (MO). **Río San Juan:** sin loc., *Hitchcock 8606* (US). VENEZUELA. **Distrito Federal:** Caracas, Antimano, *Sydow 6* (US). **Falcón:** Cerro Socopo, *Liesner et al. 8453* (MO). **Lara:** Palavecino, *Burandt V0159* (US). **Zulia:** Distr. Mara, along Río Socuyo, *Steyermark et al. 122592* (MO).

7. Paspalum campylostachyum (Hack.) S. Denham, comb. nov. Basónimo: *Panicum campylostachyum* Hack., Oesterr. Bot. Z. 51: 367. 1901. *Thrasya campylostachya* (Hack.) Chase, Proc. Biol. Soc. Washington 24: 115. 1911.

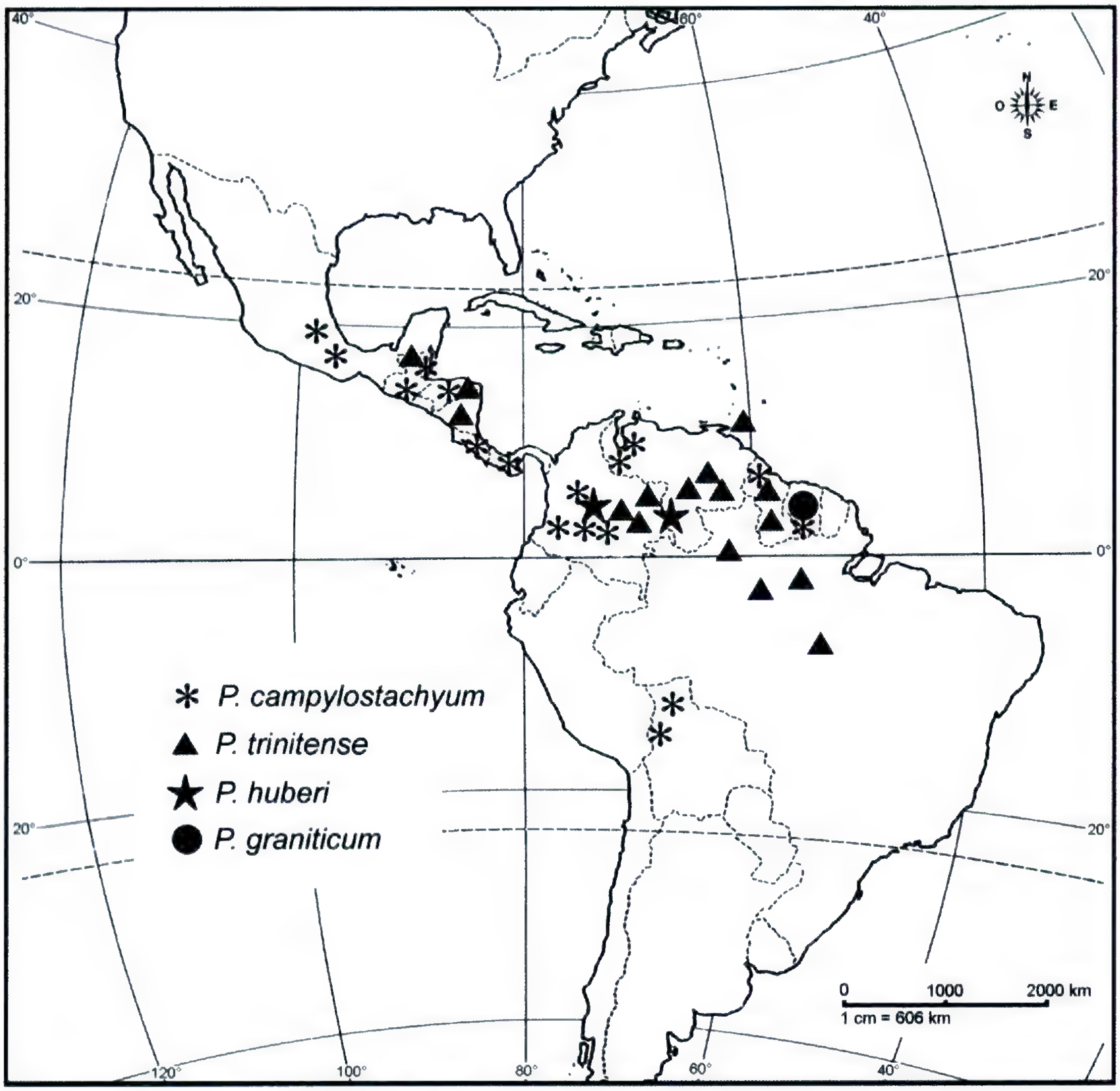

Figura 12. Distribución de *Paspalum campylostachyum, P. trinitense, P. huberi* y *P. graniticum.*

TIPO: Costa Rica. In savannis ad Cañas Gordas, Feb. 1897, *H. F. Pittier 11012* (lectotipo, designado por Chase (Proc. Biol. Soc. Washington 24: 115. 1911), W no visto; isotipos, BR!, foto SI!, CR-11012 no visto, US-824418!, US-80647 no visto).

Thrasya ciliatifolia Swallen, Ann. Missouri Bot. Gard. 30: 175. 1943. TIPO: Panamá. Zona del Canal: *A. S. Hitchcock 7988 1/2* (holotipo, US!).

Thrasya gracilis Swallen, Ann. Missouri Bot. Gard. 30: 176. 1943. TIPO: Panamá. Chiriquí: Cerro Vaca, *H. F. Pittier 5365* (holotipo, US!).

Referencias. Para descripción de la especie véase Burman (1985 [1987]); ilustración en Pohl (1980).

Número cromosómico. $n = 20$ (Davidse & Pohl, 1972a y 1972b); $2n = 40$ (Pohl & Davidse, 1971).

Distribución y ecología. Esta especie, ampliamente distribuida, habita desde México (Davidse, 1994) y Centro América hasta Venezuela, Colombia, Guyana y Surinam (Burman 1985 [1987]) y luego en Bolivia (Fig. 12); crece en pinares o bordes de bosques, es frecuente en áreas perturbadas, desde el nivel del mar a los 2100 m de elevación.

Observaciones. Paspalum campylostachyum presenta una alta variabilidad morfológica; se caracteriza por sus espiguillas de 2.7–3 mm de largo y 0.8–1 mm de ancho, y la lemma inferior 7-nervia, sulcada pero usualmente no hendida; los racimos son solitarios, de 4–10 cm de largo y 1.8–2 mm de ancho. Burman (1985 [1987]) menciona que ciertas plantas ocasionalmente presentan espiguillas con disposición tipo "paspaloide"; sin embargo no se han observado ejemplares con esta característica. Comunmente las espiguillas de esta especie son glabras; sin embargo, en los ejemplares proceden-

tes de Bolivia se observa la lemma inferior levemente ciliada.

Material representativo estudiado. BELIZE. **Stann Creek:** *Gentle 8027* (MEXU, US). **Toledo:** 16º30′N, 88º41′W, *Davidse & Brant 32492*/*** (SI). BOLIVIA. **La Paz:** Nor Yungas, Coroico, *Hitchcock 22728* (US). COLOMBIA. **Cauca:** entre Madomo y Pescador, *Zuloaga & Londoño 4188* (SI). **Meta:** Restrepo, *Zuloaga 3942* (SI). **Magdalena:** Santa Marta, *Smith 176* (US). COSTA RICA. **Cartago:** 3 km of Agua Caliente, *Pohl & Davidse 11378* (US). GUATEMALA. **Alta Vera Paz:** Finca Sepacuite, *Cook & Griggs 289* (US). HONDURAS. **Comayagua:** Sigutepeque, *Standley 56363* (US). **Olancho:** Montaña de Chifiringo, *Soto 111* (SI). PANAMÁ. **Veraguas:** San José, *Nee 8185* (US). **Zona del Canal:** entre Pedro Miguel y Corozal, *Hitchcock 7988* (US). VENEZUELA. **Lara:** Dpto. Morán, carr. Guarico–Villa Nueva, 4 km hacia Villa Nueva, *Burandt Jr. Vo138* (VEN). **Táchira:** 31 km de San Cristóbal camino a Las Delicias, alrededores del Control de Guardia Pabellón, a 2 km de Pabellón, *Morrone et al. 4702* (SI).

8. Paspalum carajasense S. Denham, nom. nov. Nombre reemplazado: *Thrasya longiligulata* C. N. Bastos & A. G. Burm., Bol. Mus. Paraense Emilio Goeldi, N.S., Bot 4(2): 236, f. 1–2. 1988. TIPO: Brasil. Pará: Marabá, Serra dos Carajás, Mina Norte 1, 19 Abr. 1985, *N. A. Rosa & M. F. F. da Silva 4691* (holotipo, MG no visto; isotipos, INPA no visto, MG no visto, RB no visto, SP no visto).

Referencias. Para descripción e ilustración de la especie véase protólogo.

Distribución y ecología. Especie conocida para Brasil, en las Sierras de Carajás, donde es frecuente sobre afloramientos rocosos (Fig. 6).

Observaciones. Es una especie anual, rastrera y enraizada en los nudos en contacto con el sustrato; los racimos miden hasta 4.5 cm de largo y son foliáceos y glabros; las espiguillas, con un callo en la base, miden 2–2.5 mm de largo, con la gluma inferior presente y la superior subigual a la espiguilla.

El epíteto específico del nombre nuevo hace referencia a la localidad geográfica donde se distribuye la especie.

Material estudiado. BRASIL. **Pará:** Serra dos Carajás, *Sperling et al. 5583*/*** (MO, US).

9. Paspalum cinerascens (Döll) A. G. Burm. & C. N. Bastos, Bol. Mus. Paraense, Emilio Goeldi, N.S. Bot. 4(2): 241. 1988. *Panicum cinerascens* Döll, Fl. Bras. 2 (2): 189. 1877. *Thrasya cinerascens* (Döll) Judz., Fl. Guianas, ser. A. Phanerog. 8(187): 631. 1990. TIPO: Brasil. Minas Gerais: *P. W. Lund s.n.* (holotipo, KR no visto; isotipo, US-2942145!). Figura 13.

Thrasya reticulata Swallen, Contr. U.S. Natl. Herb. 29(2): 267. 1949. Syn. nov. Non *Paspalum reticulatum* Hack., Oesterr. Bot. Z. 51: 199. 1901. *Paspalum multinervium* A. G. Burm., Acta Bot. Venez. 14(4): 90. 1985 [1987]. TIPO: Brasil. Maranhão: between Barra do Corda and Grajahú, *J. R. Swallen 3665* (holotipo, US-1612976!, foto SI!).

Plantas perennes, cespitosas, rizomas de entrenudos cortos; *cañas* de (80–)100–190 cm de alto, 0.3–0.5 cm de diámetro, erectas, simples a ramificadas en nudos inferiores o medios; entrenudos de 12–28 cm de largo, cilíndricos, rígidos, densamente vilosos a papiloso-hirsutos, más densamente hacia la porción superior, los apicales glabrescentes, en ocasiones glabros en toda la caña; nudos castaños, pilosos a densamente barbados. *Vainas* inferiores más largas que los entrenudos, superpuestas, las superiores usualmente más cortas que los entrenudos, aquilladas en la porción superior, densamente vilosas, con pelos plateados a papiloso-hirsutas en las vainas basales y medias, las apicales pilosas a glabrescentes, en ocasiones glabras en toda la caña, los márgenes cortamente pestañosos a densamente vilosos, con pelos largos; *lígulas* membranáceas, de 1–2 mm de largo, castañas, lustrosas; seudolígula ausente o con cortos pelos de 1.5–2 mm de largo; cuello castaño, piloso; *láminas* linear-lanceoladas, de 20–50 cm de largo, 0.8–2 cm de ancho, las apicales más cortas, rígidas, planas o con los márgenes involutos, atenuadas hacia la base, raro de base redondeada, el ápice acuminado, de pilosidad variable, glabras, pubescentes a densamente pilosas en ambas caras, o la abaxial pilosa y la adaxial glabra, los márgenes escabrosos. *Pedúnculos* 1–2(3) en la última vaina foliar, subincluidos a exertos, o uno de ellos completamente incluido en la vaina, hasta de 46 cm de largo, cilíndricos, glabros a esparcidamente pilosos. *Inflorescencias* terminales y axilares en la última vaina foliar; racimos 1–7, solitarios o alternos, ascendentes; eje principal ausente o de 4–8 cm de largo, glabro; pulvínulos pilosos; raquis de los racimos de 9–32 cm de largo, 0.7–1 mm de ancho, triquetro, glabro a regularmente piloso en los márgenes, con pelos de 2–4 mm de largo, los márgenes escabrosos, terminando en una espiguilla desarrollada; pedicelos en pares, desiguales, el de la espiguilla superior de (0.6–)0.8–1(–2) mm de largo, libres o adnatos en 1/2(–2/3) de su longitud, escabrosos, glabros a pilosos, con pelos sedosos hasta de 2 mm de largo, en ocasiones con un breve borde membranáceo en el ápice; espiguillas no imbricadas a imbricadas, dispuestas en 1–4 series. *Espiguillas* elipsoides, de (2.1–)3–4.2 mm de largo, 1–1.6(–2) mm de ancho, cóncavo-convexas, reticuladas hacia

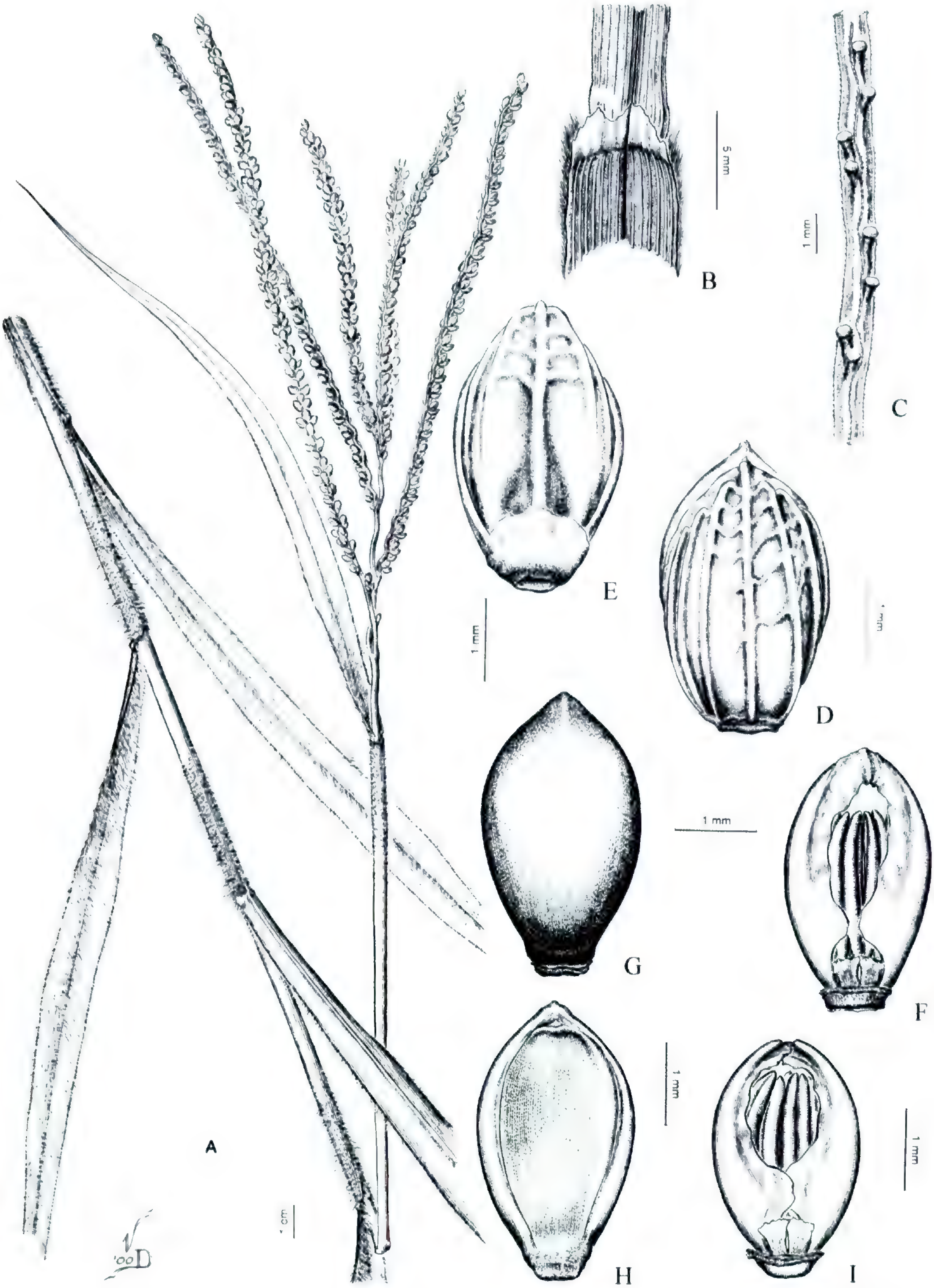

Figura 13. *Paspalum cinerascens.* —A. Hábito. —B. Detalle de la lígula. —C. Porción del raquis de los racimos, pedicelos. —D. Espiguilla, vista dorsal mostrando la gluma superior. —E. Espiguilla, vista ventral mostrando la gluma inferior y lemma inferior. —F. Pálea inferior, lodículas y estambres. —G. Antecio superior, vista dorsal mostrando la lemma. —H. Antecio superior, vista ventral mostrando la pálea. —I. Pálea superior, lodículas y estambres. (A–I, *Irwin et al. 11259.*)

el ápice, verdosas a pálidas, glabras a escasamente pilosas; *gluma inferior* dimorfa: ancha y de ápice obtuso, 1/4(–1/2) del largo de la espiguilla, centrada, glabra, enervia o 1-nervia en la espiguilla superior del par; lanceolada a acuminada, 1/2–2/3 del largo de la espiguilla, excéntrica, glabra, 1–3-nervia, en la espiguilla basal; *gluma superior* subigual a la espiguilla, membranácea, no papilosa, glabra a corta y escasamente pilosa hacia el ápice, fuertemente reticulada en la porción superior, 7–9-nervia, los tres nervios centrales mucronados en el ápice, los nervios fuertemente marcados y equidistantes; *lemma inferior* tan larga como la espiguilla, coriácea, glabra, con el dorso fuertemente sulcado y papiloso, el ápice ocasionalmente retuso, 5(7)-nervia, los nervios endurecidos y equidistantes, con vénulas transversales hacia la porción distal, los márgenes curvos sobre la pálea inferior; *pálea inferior* tan larga como su correspondiente lemma, hialina, con los nervios endurecidos; *flor inferior* estaminada; estambres 3, anteras de 1.5–1.7 mm de largo; *antecio superior* anchamente elipsoide a obovoide, de 2.3–3.5 mm de largo, 1–1.8 mm de ancho, cartáceo, plano-convexo a cóncavo-convexo, pajizo a grisáceo, lemma y pálea con células cuadradas, de paredes onduladas, con papilas verrugosas regularmente distribuidas, centradas en las células, con 4–6 verrugas cada una, micropelos hacia el ápice de la lemma y márgenes apicales de la pálea, con la célula apical de igual largo que la basal o 1.5 veces más larga, macropelos unicelulares hacia el ápice de lemma y pálea; lodículas de 0.3–0.5 mm de largo; estambres 3, anteras de 1.6–1.8 mm de largo. *Cariopsis* no vista.

Distribución y ecología. Habita desde Venezuela, Guayana Francesa y Brasil, hasta Bolivia y Paraguay (Fig. 11). Crece en márgenes de bosques o en cerrados, sobre suelos rojos, arenosos o rocosos o en cursos de agua; desde el nivel del mar hasta 1100 m.

Observaciones. *Paspalum cinerascens* se caracteriza por sus espiguillas fuertemente reticuladas en el dorso de la gluma superior y reticulada en el ápice de la lemma inferior, siendo la lemma inferior fuertemente sulcada y la pálea inferior tan larga como su lemma, con la flor inferior estaminada.

Esta especie es variable en el número de racimos por inflorescencia; usualmente presenta un racimo solitario o dos alternos, aunque algunos ejemplares del centro de Brasil (*Chase 10844*, *Irwin 11259* y *12076*) presentan 3–6 racimos, mientras que en los especímenes de Paraguay se observan 5–7 racimos por inflorescencia. La pilosidad de las espiguillas también es variable: comúnmente son glabras (como por ejemplo en los ejemplares *Zardini & Zavala 44193*, *Chase 10844*, *Irwin et al. 12994*); o en ocasiones son pilosas, con unos poco pelos junto al ápice de la gluma superior (*Chase 11677*, *Montes 3032*). A su vez, la pilosidad en cañas, vainas y láminas varía de densamente vilosas, con pelos plateados a glabras en *Chase 10844*, *Egler & Raimundo 1473* y *Cremers 12348*. En ocasiones los pedicelos presentan un borde membranáceo en el ápice, como en *Irwin et al. 16337* y *Cremers 12348*. Existen variaciones en el pedicelo superior en cuanto al largo y su relación con el raquis; éste puede ser corto y libre (*Hoff & Cremers 6504* o *Irwin et al. 12076*) o elongado y parcialmente adnato al raquis (hasta 2 mm de largo en *Chase 10931*; adnato 1/2 de su longitud en *Swallen 3694*, *Irwin et al. 11259*, *Chase 10844* y *Granville et al. 12240*; adnato en 2/3 de su longitud en *Cremers 12348* y *Zardini & Zavala 44193*, en estos últimos ejemplares las espiguillas se disponen en 1 serie sobre el raquis). En el material tipo, *Lund s.n.*, los pedicelos son cortos y adnatos en 3/4 de su longitud y la posición de las espiguillas es "paspaloide." En *Cremers 12348* y *Granville et al. 12240* las espiguillas se presentan en posición "paspaloide," o bien en posición "thrasyoide" en un mismo racimo.

Paspalum cinerascens ha sido relacionado con especies de *Thrasya* por presentar pedicelos frecuentemente elongados y parcialmente adnatos al raquis, por la posición ocasionalmente "thrasyoide" de las espiguillas y por la lemma inferior fuertemente sulcada. Así, Burman (1985 [1987]), relaciona a esta especie con las especies no especializadas de *Thrasya* y Judziewicz (1990), por otra parte, considera a *Paspalum cinerascens* como *Thrasya cinerascens*.

Judziewicz (1990) diferencia a *Thrasya cinerascens* [= *Paspalum cinerascens*] de *T. reticulata* [= *Paspalum multinervium*] por el tamaño y forma de las espiguillas (3.3–4.2 × 1.8–2.5 mm, ovadas-elipsoides vs. 2.5–3 × 0.8–1.2 mm, angostamente elipsoides a ligeramente obovadas), el largo de los racimos (15–25 cm vs. (5–)7–16 cm) y el ancho del raquis (1–1.7 mm vs. 0.4–0.7 mm). En el material tipo de *T. reticulata* se observan espiguillas no túrgidas, de 3–3.3 mm de largo y 1–1.4 mm de ancho y racimos de 16–21 cm de largo y 0.8 mm de ancho en el raquis. Por otra parte, en un fragmento del isotipo de US de *P. cinerascens*, las espiguillas son túrgidas, de 3.2–3.5 mm de largo y 1.5–1.6 mm de ancho y el raquis de los racimos es de 1 mm de ancho. El análisis del material de herbario permitió observar que existe un continuo en el tamaño de las espiguillas y que los ejemplares tipo se ubican

dentro de esta variación. Consecuentemente, se considera a *T. reticulata* sinónimo de *P. cinerascens*.

Material representativo estudiado. BOLIVIA. **Santa Cruz:** Ñuflo de Chávez, Par. Nac. Noel Kempff, Los Fierros 5 km al NE de la carr., *Killeen et al. 5645* (MO). BRASIL. **Amapá:** Inselberg, Talou 2 km Massiffdes, *Granville et al. 12240* (MO). **Distrito Federal:** ca. 25 km E of Brasília, *Irwin et al. 12994** (CTES, MO); vic. of Paranoá, *Irwin et al. 11259* (MO, US); ca. 25 km E of Brasília, *Irwin et al. 12076* (MO, US). **Goiás:** Rio dos Bois, *Chase 11677* (MO, US). **Maranhão:** Barra do Corda to Grajahú, *Swallen 3694* (US). **Mato Grosso:** Campo Grande, *Chase 10844*** (MO); ca. 86 km N of Xavantina, *Irwin et al. 16337* (MO, US); S of Lagoinhas, betw. Campo Grande and Dourados, *Chase 10931* (US). **Pará:** Conceçiao do Araguaia, *Plowman et al. 9098* (MO). **Paraná:** Mun. Campo Morão, E do Aeroporto, *Hatschbach 8813* (US). **Piauí:** sin loc., *Gardner 3508* (US). **Roraima:** Serra dos Surucucus, *Prance et al. 9901* (MO). **São Paulo:** Jundiahy, cerca São Paulo, *Hoehne 9854* (US). GUAYANA FRANCESA. **Cayena:** savane Roche du Quatorze Juillet-bassin du Oyapock, *Cremers 12348* (MO, US); Savane Mamaribo, *Hoff & Cremers 6504* (US). PARAGUAY. **Amambay:** Par. Nac. Cerro Corá, cerrado al pie del Cerro Alambique, *Zuloaga & Morrone 7305* (SI). **San Pedro:** Yaguareté forest, *Zardini & Zavala 44193* (MO, SI). VENEZUELA. **Anzoátegui:** Morichal El Piñal, 3 km N de Santiago de Cabrutica, *Montes 3032* (MO).

10. Paspalum crucense (Killeen) S. Denham, comb. nov. Basónimo: *Thrasya crucensis* Killeen, Ann. Missouri Bot. Gard 77: 190. 1990. TIPO: Bolivia. Santa Cruz: Ñuflo de Chávez, Rancho Puesto Nuevo, 26 Feb. 1987, *T. Killeen 2334* (holotipo, ISC no visto; isotipos, F no visto, LPB no visto, MO!, SI!, SP no visto, US!).

Referencias. Para descripción e ilustración de la especie véase protólogo.

Número cromosómico. $2n = 20$ (Killeen, 1990; Norrmann et al., 1994).

Distribución y ecología. Especie endémica de Bolivia, crece en el cerrado, formando densas matas, sobre suelos arenosos y rocosos (Fig. 6).

Observaciones. *Paspalum crucense* presenta, al igual que *P. foliiforme*, *P. setosum* y *P. huberi*, racimos con los márgenes glabros, espiguillas con un callo en la base y la lemma inferior sulcada y hendida con pelos conspicuos. En esta especie las vainas son glabras y se observan aurículas en su ápice; las lígulas miden hasta 5 mm de largo.

Material estudiado. BOLIVIA. **Santa Cruz:** Ñuflo de Chávez, *Killeen 1819*/*** (MO, US).

11. Paspalum cultratum (Trin.) S. Denham, comb. nov. Basónimo: *Panicum cultratum* Trin., Gram. Panic. 126. 1826. *Thrasya cultrata* (Trin.) Nees, Fl. Bras. Enum. Pl. 2: 95. 1829. TIPO: Brasil. Minas Gerais: Congonhas do Campo, *G. H. von Langsdorff s.n.* (holotipo, LE!, foto SI!; isotipo, US!). Figura 14.

Plantas perennes, cespitosas, rizomas de entrenudos cortos, robustos, cubiertos por catáfilos pilosos; *cañas* de 85–115(–160) cm de alto, 2–3(–4) mm de diámetro, erectas, simples a ramificadas en los nudos basales o medios; entrenudos de 11–19 cm de largo, los basales con pelos papilosos, densos o esparcidos, los apicales glabros; nudos castaños, glabros. *Vainas* más largas que los entrenudos, superpuestas en la base, las basales pilosas o papilo-pilosas a glabras y las apicales glabras a glabrescentes, los márgenes densamente pestañosos; *lígulas* membranáceas, de 0.5–0.7 mm de largo; seudolígulas con pelos de 4–5 mm de largo; cuello piloso a barbado; *láminas* linear-lanceoladas, de 10–25(–40) cm de largo, 0.6–1.2 mm de ancho, las apicales más cortas a reducidas, planas a plegadas, con frecuencia parcialmente laciniadas, de base atenuada y ápice agudo, densamente pilosas en la cara abaxial y glabrescentes en la adaxial, los márgenes escabrosos y pestañosos, el nervio medio carinado. *Pedúnculos* 1–2 en la última vaina foliar, cortamente exertos a exertos o uno de ellos completamente incluido en la vaina, hasta de 35 cm de largo, filiformes, densamente piloso hacia la porción apical; ocasionalmente pedúnculos presentes en las vainas subapicales. *Inflorescencias* terminales y axilares; racimo 1, levemente arqueado; eje principal nulo; pulvínulos castaños, pilosos; raquis de los racimos de 13–22(–27) cm de largo, 0.9–1.5 mm de ancho, triquetro a terete, con dos brevísimas alas, en ocasiones con la primer porción (ca. 1 cm) sin espiguillas, glabra o densamente pilosa, luego glabro, terminando en una espiguilla desarrollada; pedicelos en pares, desiguales, el de la espiguilla superior hasta de 1 mm de largo, híspidos a escabrosos; espiguillas imbricadas, dispuestas en 4 series sobre el raquis. *Espiguillas* elipsoides, de 3.2–3.7(–3.9) mm de largo, (1.2–)1.5–1.7 mm de ancho, cóncavo-convexas, pálidas a verdosas en los nervios, glabras a apenas cilioladas; *gluma inferior* dimorfa: triangular y de ápice agudo a obtuso, 1/4–1/3 del largo de la espiguilla, glabra o ciliolada en los márgenes, centrada a excéntrica, enervia en la espiguilla superior del par; lanceolada y de ápice acuminado, 1/2 del largo de la espiguilla, glabra o con macropelos en el ápice, excéntrica, 1-nervia, con el nervio escabroso en la espiguilla inferior del par; *gluma superior* de 1/2–2/3(–3/4) del largo de la espiguilla, papirácea, glabra o corta y esparcidamente pilosa en la superficie, ocasionalmente con cilias en los márgenes basales, con un corto

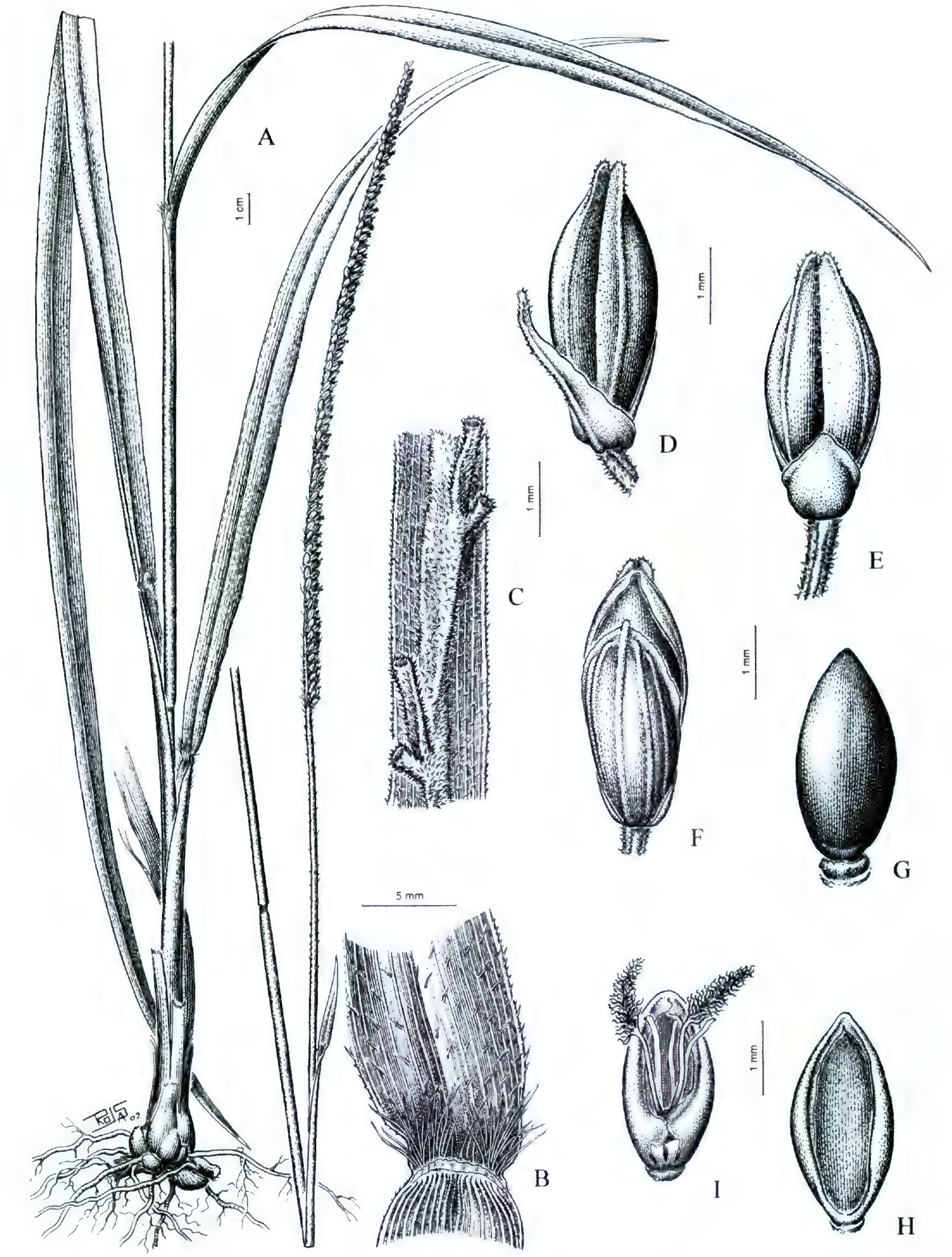

Figura 14. *Paspalum cultratum.* —A. Hábito. —B. Detalle de la lígula. —C. Porción del raquis de los racimos, pedicelos. —D. Espiguilla inferior, vista ventral mostrando la gluma inferior y lemma inferior. —E. Espiguilla superior, vista ventral mostrando la gluma inferior y lemma inferior. —F. Espiguilla, vista dorsal mostrando la gluma superior. —G. Antecio superior, vista dorsal mostrando la lemma. —H. Antecio superior, vista ventral mostrando la pálea. —I. Pálea superior, lodículas y gineceo. (A, *Chase 10229*; B–I, *Chase 8972*.)

margen hialino, 5-nervia, con los nervios equidistantes a próximos entre sí, el central mucronado o no; *lemma inferior* tan larga como la espiguilla, coriácea, papilosa, sulcada, en ocasiones hendida en el nervio medio a la madurez, glabra o corta y esparcidamente pilosa en la superficie, el ápice retuso y con macropelos, los márgenes doblados o no sobre el antecio, 5-nervia, un nervio central y los restantes marginales, próximos entre sí o equidistantes; *pálea inferior* subigual a la lemma, hialina, con los nervios endurecidos; *flor inferior* estaminada o perfecta; estambres 3, anteras de 3 mm de largo; *antecio superior* elipsoide, de 3.1–3.5 mm de largo y 1–1.5 mm de ancho, la lemma sobrepasando el ápice de la pálea, plano-convexo a ligeramente cóncavo-convexo, crustáceo, pajizo a grisáceo, lemma y pálea con células cuadradas, de paredes onduladas, con papilas verrugosas distribuidas en hileras regulares, centradas en las células, con 4–6 verrugas en cada célula, lemma con micropelos bicelulares en el ápice, con la célula apical dos veces más larga que la basal; lodículas 0.2 mm de largo; estambres 3, anteras de 2.9 mm de largo, ocasionalmente desarrolladas. *Cariopsis* no vista.

Distribución y ecología. *Paspalum cultratum* es endémica de Minas Gerais, Brasil (Fig. 11). Habita en bosques, selvas en galería y campos abiertos, en afloramientos rocosos o suelos arenosos o arcillosos, entre 1200–1500 m s.m.

Observaciones. *Paspalum cultratum* se caracteriza por sus racimos solitarios, con el raquis triquetro a terete y los pedúnculos densamente pilosos hacia el ápice, la gluma superior más corta que la espiguilla, 5-nervia con los márgenes equidistantes a próximos entre sí, y la lemma inferior sulcada o hendida a la madurez, con el ápice retuso y con macropelos.

Las vainas basales son persistentes y protegen la base de la planta como adaptación a los fuegos frecuentes.

El ejemplar *Chase 8671* es un espécimen robusto, de 160 cm de alto, con cañas de 4 mm de diámetro, láminas de 40 cm de largo, racimos de 27 cm de largo y espiguillas de 3.9 mm de largo y 1.6 mm de ancho.

Esta especie es afín a *Paspalum unispicatum* por sus racimos solitarios, la forma de las láminas y las espiguillas con gluma inferior dimorfa. *Paspalum unispicatum* se diferencia por sus rizomas de entrenudos alargados, por la lemma inferior no hendida, usualmente sulcada, lisa a finamente papilosa y la gluma superior tan larga como la espiguilla o, en ocasiones, dejando al descubierto el dorso apical de la lemma superior, los pedúnculos glabros y el raquis de los racimos no terete.

Paspalum monostachyum es otra especie con racimos solitarios y raquis de los racimos triquetro a terete, pero sus rizomas alargados, arqueados y sus láminas macizas permiten diferenciarla de las especies antes mencionadas.

La lemma inferior hendida por el nervio medio es una característica común del género *Thrasya*, y por esta razón *P. cultratum* ha sido previamente tratado bajo ese género (Chase, 1911).

Burman (1985 [1987]) transfiere *Thrasya cultrata* a *Paspalum*; sin embargo, la nueva combinación no es válida de acuerdo con el artículo 33.3 del Código Internacional de Nomenclatura Botánica (Greuter et al., 2000) debido a que el autor no indicó la cita de la publicación original de *Panicum cultratum* Trin.

Material estudiado. BRASIL. **Minas Gerais:** Serra Mantiqueira, Barbacena, *Chase 8651** (US); Serra Mantiqueira, Barbacena, *Chase 8671* (US); Cachoeira da Campo, *Glaziou 20562* (US); Carandaí, Crespo, *Duarte 5068* (US); Hargreaves, *Chase 10229* (US); Serra do Curral, SE of Bello Horizonte, *Chase 8972* (US); Serra do Espinhaço, ca. 12 km W of Barao de Cocais, *Irwin et al. 29335*** (MO).

12. Paspalum decumbens Sw., Prodr. 22. 1788. *Panicum decumbens* (Sw.) Roem. & Schult., Syst. Veg. 2: 429. 1817. TIPO: Jamaica. *O. P. Swartz s.n.* (holotipo, S no visto; isotipos, B no visto, G no visto, M!, P no visto, US-2854654 no visto).

Dimorphostachys pedunculata (Poir.) E. Fourn., Mex. Pl. 2: 15. 1886. *Paspalum pedunculatum* Poir., Encycl. 4: 315. 1816. TIPO: Guayana Francesa. Cayenne: *sin colector, s.n., Herb. Desfontaines* (holotipo, FI no visto; isotipos, P no visto, US-2942523!).

Paspalum vaginiflorum Steud., Syn. Pl. Glumac. 1: 19. 1853. TIPO: Guayana Francesa. *Herb. Lenormand "Guyana n° 7"* (holotipo, P!; isotipo, US-80044 no visto).

Plantas perennes; rizomas de entrenudos cortos, *cañas* apoyantes a decumbentes o arraigadas en los nudos basales, la porción erecta de 15–50 cm de alto, 1–3 mm de diámetro, plurinode, laxamente ramificada; entrenudos de 3–10 cm de largo, ligeramente comprimidos, finamente estriados, glabros; nudos pilosos, castaños, comprimidos. *Vainas* de 2–5 cm de largo, aquilladas en la porción superior, glabras a esparcidamente pilosas, los márgenes pestañosos; *lígulas* membranáceas, de 0.8–1.2 mm de largo; seudolígula ausente o presente, con escasos pelos hasta de 2 mm de largo; cuello glabro, castaño; *láminas* lanceoladas a linear-lanceoladas, de 3.5–8(–10) cm de largo, 0.4–1 cm de

ancho, herbáceas, planas, de base redondeada, contraida en la unión con la vaina, ápice agudo, cara adaxial cortamente pubescente, la abaxial glabra, o con ambas caras pilosas, nervio medio aquillado. *Pedúnculos* 1–8 en la última vaina foliar, exertos a parcialmente incluidos, hasta de 18 cm de largo, filiformes, acanalados, glabros a cortamente pilosos; frecuentes en los nudos medios. *Inflorescencias* terminales y axilares; racimos 1, arqueado; eje principal nulo; pulvínulos pilosos; raquis de los racimos de 1–3.5 cm de largo, 0.3–0.5 mm de ancho, triquetro, con los márgenes curvos, glabro a esparcidamente piloso, escabriúsculo, terminando en una espiguilla desarrollada; pedicelos en pares, subiguales, de 0.6–0.8 mm de largo, híspidos; espiguillas distribuidas en 2–4 series irregulares. *Espiguillas* obovoides, de 1.2–1.8 mm de largo, 1–1.1 mm de ancho, plano-convexas, de ápice apiculado, verdosas a pajizas, en ocasiones con tintes violáceos, glabras; *gluma inferior* dimorfa: ancha y de ápice obtuso, hasta 1/3 del largo de la espiguilla, centrada, glabra, enervia a 1-nervia en la espiguilla superior del par; triangular y de ápice agudo a obtuso, (1/3–)1/2–2/3 del largo de la espiguilla, excéntrica, glabra, enervia a 1-nervia, en la espiguilla inferior; en ambas espiguillas la gluma inferior con base ancha, abrazando a la lemma inferior; *gluma superior* 1/2 (raro 3/4) del largo de la espiguilla, dejando al descubierto el ápice del antecio superior, glabra, no papilosa, 3–5-nervia, con un nervio medio y los marginales, próximos entre sí a equidistantes; *lemma inferior* tan larga como la espiguilla, finamente papilosa, glabra, membranácea a cartácea, no sulcada, 5-nervia, con un nervio medio y los marginales próximos entre sí, con los márgenes doblados sobre el antecio; *pálea inferior* ausente o 1/2–3/4 del largo de la espiguilla, hialina, con los nervios endurecidos; *flor inferior* ausente o presente, cuando presente, con 3 estambres, anteras de 0.5 mm de largo; *antecio superior* obovoide, de 1.2–1.7 mm de largo, 1–1.1 mm de ancho, plano-convexo, crustáceo, pajizo; lemma y pálea con células cuadradas, de paredes onduladas, con papilas verrugosas distribuidas regularmente en toda la superficie, centradas, con 2–4 verrugas cada una; lodículas de 0.1–0.2 mm de largo; estambres 3, anteras ca. 0.5 mm de largo. *Cariopsis* subesférico, de 0.9 mm de largo, 0.8 mm de ancho; hilo elíptico, 1/3–1/2 de la cariopsis; embrión 1/3 del largo de la espiguilla.

Iconografía. S. A. Renvoize, Gramíneas de Bolivia: 483, fig. 105, A–c. 1998.

Número cromosómico. $n = 10$ (Davidse & Pohl, 1972a, 1978).

Distribución y ecología. *Paspalum decumbens* se distribuye desde el sur de México, el Caribe y América Central hasta Bolivia y Brasil (Fig. 15). Habita en bosques, selvas y campos abiertos, en lugares sombríos, a lo largo de arroyos y ríos, en suelos rocosos, sueltos, lateríticos o arcillosos; es frecuente en áreas perturbadas, en cultivos, a lo largo de vías o caminos, también se la ha hallado como epífita sobre troncos de árboles. Crece desde el nivel del mar a los 3200 m de altura.

Observaciones. Esta especie se caracteriza por poseer 1–8 pedúnculos en la última vaina foliar, racimos solitarios, arqueados, de 1–3.5 cm de largo, espiguillas obovoides y apiculadas, con la gluma superior 1/2 (raro 3/4) de la espiguilla.

Especie afín a *P. nutans*, ésta última se distingue por tener espiguillas usualmente sin la gluma inferior, cuando presente de hasta 1/6 del largo de la espiguilla, mientras que en *P. decumbens* siempre esta presente y es mayor a 1/6 de la espiguilla.

En el ejemplar *Schultes & Cabrera 17408* (US) se observan pedicelos con ramificaciones de 2º, 3º y 4º orden y las espiguillas dispuestas en varias series; el espécimen *Archer 2134* (US) presenta un racimo ramificado en su base y pedicelos con ramificaciones hasta de 3º orden.

Material representativo estudiado. BELIZE. **Stann Creek:** North Branch Section, Humming Bird Hwy., *Gentle 9229* (G, MEXU, MO). **Toledo:** Bladen Nat. Res., *Davidse 35920* (MEXU). BOLIVIA. **La Paz:** Mapiri, *Buchtien 84* (US). **Santa Cruz:** Ichilo, Montero to Puerto Grether, E de Cochabamba, *Renvoize & Cope 3955* (US). **Cochabamba:** J. C. Torrico, Río Blanco, *Seidek 3596* (LPB). BRASIL. **Acre:** Subbase de Cruzeiro do Zul-divisa Brasil-Perú, Ponto 01-SC-18-XA, *Marinho 324* (MO). **Amazonas:** 15 km of Borba, *Hill et al. 12801* (K, MO, US). **Distrito Federal:** Parque Municipal do Gama, *Irwin et al. 10196* (MO). **Espírito Santo:** Mun. Linhares, Reserva Biologica de Sooetama, *Zuloaga et al. s.n.* (MO-3638058). **Goiás:** Serra Dourada, ca. 30 km SE of Goiás Velho, *Irwin et al. 11889* (K, MO, US). **Mato Grosso:** bet. Rondonopolis and São Lourenço, *Chase 12000* (US). **Minas Gerais:** Viçosa, *Chase 9510* (US). **Pará:** Belterra, *Black 1819** (US). **Rio de Janeiro:** Camino dos Macacos, *Chase 9974* (US). **Santa Catarina:** Botuverá, Águas Negras, *Klein & Bresolin 11702* (US). **São Paulo:** Mun. Iguape, centro of Iguape Island, *Clayton & Eiten 4760* (US). COLOMBIA. **Amazonas:** Río Igará-Paraná, corr. La Chorrera, *Gasche & Desplats 109* (G). **Antioquia:** along road bet. San Luis and Puerto Triunfo, ESE of Medellín, SE of Granada, *Croat 52033* (MO). **Boyacá:** 2 km de Toca hacia Pesca, *Zuloaga 3871* (SI). **Caquetá:** Cordillera Oriental, 62 km SE of Guadalupe, km Post 69 along road from Altamra to Florencia, *Davidse et al. 5635* (MO). **Chocó:** Tutunendo, *Archer 2134*** (US). **Córdoba:** Dagua Valley, *Pittier 535* (US). **Cundinamarca:** San Francisco, carretera a Pacho, *García-Barriaga 10985* (US). **Magdalena:** Santa Marta, *Smith 2157* (BM, K, P, US). **Meta:** de Cumaral a San Nicolás, 10 km del desvío a San Nicolás, *Zuloaga 3872* (MO, SI). **Nariño:** Mun. Barba-

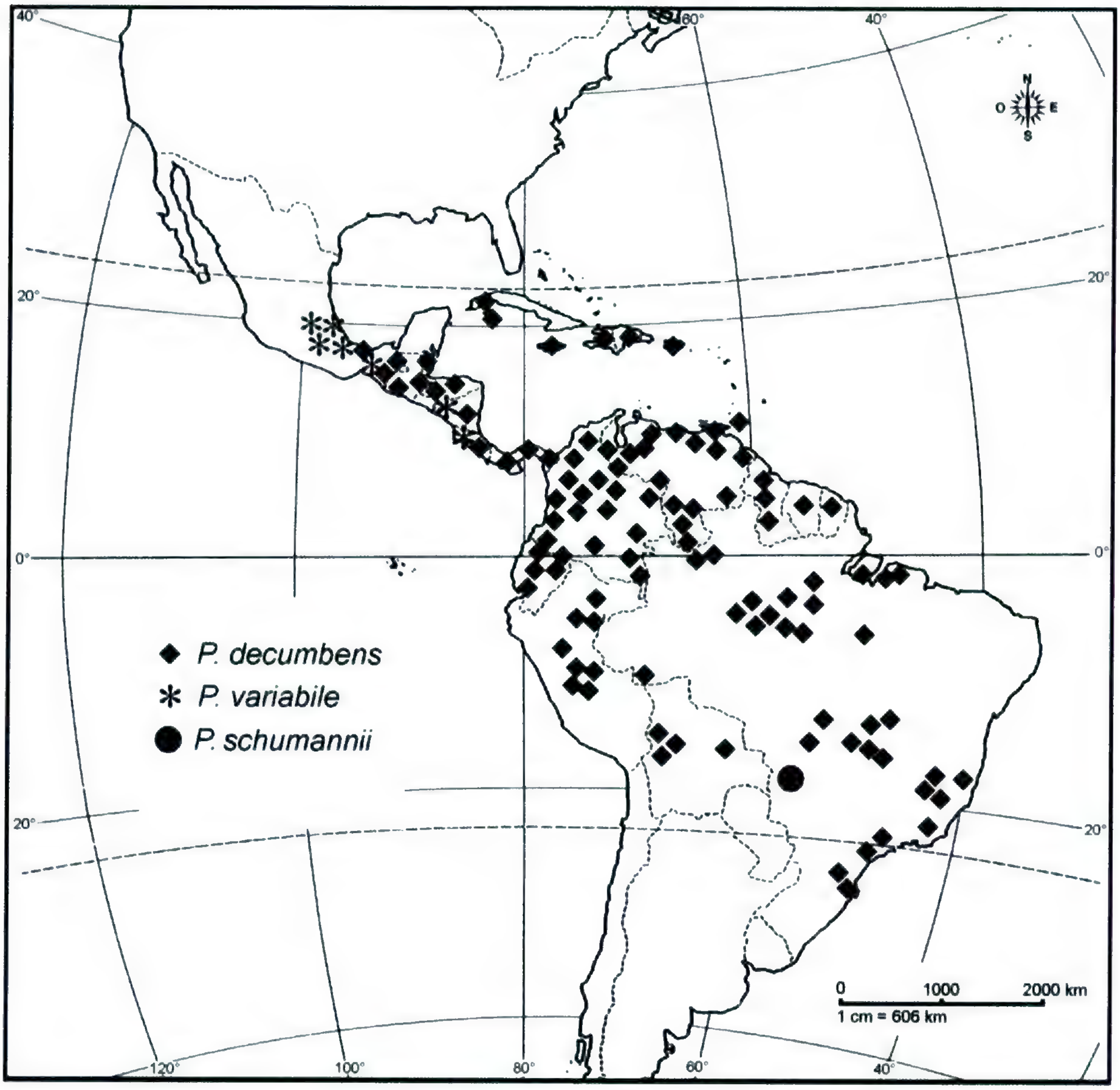

Figura 15. Distribución de *Paspalum decumbens*, *P. variabile* y *P. schumannii*.

coas, Corregimiento de Junín, a 3 km del pueblo, *Benavides 9995* (MO). **Putumayo:** Mocoa, *Gamía 4587* (US). **Santander:** Magdalena Valley, *Gentry & Renteria 20092* (MO). **Valle del Cauca:** Buenaventura, quebrada de Santa Ana, *Cuatrecasas 21036* (US). **Vaupés:** Río Piraparaná, *Schultes & Cabrera 17408* (US). **Vichada:** ca. 35 km E of Las Gaviotas along unimproved dirt road to Santa Rita, *Davidse & Llanos 5217* (MO). COSTA RICA. **Alajuela:** Reserva Biológica Monteverde Cantó de San Ramón, Río Peña Blancas Valley, *Haber et al. 11281* (MO). **Cartago:** 20 km below Turrialba on Siquirres Rd., *Pohl 10313* (MEXU). **Guanacaste:** 4 km N of Río Narango, on road to Upala, *Pohl & Lucas 13058* (MO). **Heredia:** bet. Río Peje and Río Saedinalito, *Grayum 6775* (MO, SI). **Limón:** 6 km W of Guapiles, *Pohl & Calderón 10015* (MO). **Puntarenas:** high road out of Rincón de Osa, ridge top, Rincón to 5 km W of Rincón, *Liesner 2120* (MO). CUBA. **Isla de la Juventud:** Nueva Gerona, towards Mc Kinley, *Ekman 11709* (G). **Pinar del Río:** *Ekman 11038* (US). ECUADOR. **Carchi:** NW side of Río Gualpi Chico, 25 Ene. 1988, *Hoover et al. 3027* (MO). **Guayas:** Bucay, *Asplund 5834* (US). **Imbabura:** Lita, *Acosta Solís 12154* (US). **Los Ríos:** Hacienda Clementina on Río Pita, *Asplund 5598* (G, K, US). **Napo:** Tena, *Asplund 8975* (US). **Pastaza:** along Cajabamba–Mariscal road departing main Tema–puyo road at km 31 N of Puyo, *Croat 58927* (MO, SI). **Pichincha:** 7 km E of km 7 on Hwy. Sto. Domingo–Quevedo, *Dodson et al. 7974* (MO). **Tungurahua:** valley of Río Pastaza, La Victoria, *Asplund 8537* (US). GUATEMALA. **Alta Verapaz:** sin loc., Oct. 1906, *von Tuerckheim 11452* (MO). **Izabal:** vic. of Quiriguá, *Standley 23905* (MO). **San Marcos:** Finca Armenia, San Rafael, Pie de la Cuesta to hydro-electric plant, *Dwyer 15246* (MO). GUAYANA FRANCESA. **Cayena:** Cayena, *Hoock 1302* (US). GUYANA. Kaugaruma, Potaro river, *Abraham 346* (US). HAITÍ. Artibonite, vic. of Kalacroix, Sec. Dessalines, *Leonard 7855* (MO). HONDURAS. **Atlántida:** Lancetilla Botanical Garden, S of Tela, *Pohl & Gabel 13819* (MO). **Cortés:** Montaña de La Nieve, lado SW del caserío El Tapiquilar, 20 km S de San Antonio de Cortés, *Nelson et al. 7949* (MO, SI). **Yoro:** Cordillera Nombre de Dios, hills S of San José de Texiguat, *Davidse et al. 34493* (MO). JAMAICA. Portland, Ecclesdown, *Adams 7609* (MO). MÉXICO. **Chiapas:** Ocosingo, *Reyes Garcia & Challenger 2575*

(MEXU). **Veracruz:** Catemaco 5 km, al E de Pen De Moreno, *Ortíz 1078* (MEXU, MO). NICARAGUA. **Zelaya:** 0–1 km N of San Martín, *Nee 27813* (MEXU, MO). PANAMÁ. **Bocas de Toro:** N of Cerro Brujo and Bahía de Green on the mainland, *Peterson & Annable 7199* (MO). **Coclé:** base of cerro Tife, *Knapp 3703* (MEXU). **Colón:** ca. 6.5 km from Boyd–Roosvelt Hwy., *Mori & Kallunki 2127* (K, MO). **Darién:** vic. of upper gold mining camp of Tyler Kittredge on headwaters of Río Tuquesa, *Croat 27212* (MO). **Herrera:** 10 mi. S Ocu, *Tyson et al. 2849* (MO). **Panamá:** 5 km N of Pan. Am. Hwy. at El Llano, *Nee 7875* (MO). **Veraguas:** 4 km W of Colonia Penal, *Antonio 2241* (MO). PERÚ. **Huánuco:** Tingo María, *Allard 20613* (US). **Junín:** Colonia Perené, *Hitchcock 22066* (US). **Loreto:** Yarina Cocha, *Ayala & Origgi 5923* (MO). **Pasco:** Oxapampa Iscozacim, *Smith & Salick 8339* (MO). **San Martín:** Tingo María, *Allard 21595* (US). **Ucayali:** C. Portillo, Bosque Nac. de von Humboldt, km 86, Pucallpa–Tingo María, *Gentry 29469* (MO). PUERTO RICO. Maricao, *Chase 6235* (US). REPÚBLICA DOMINICANA. **La Vega:** 23 km E of El Río along road to Santiago–Sto. Domingo Hwy., *Davidse 2682* (MO). SURINAM. Sin loc., 23 Mar. 1951, *Geyskes 68* (US). TRINIDAD Y TOBAGO. Erin Savannas, near Buenos Ayres, *Cowan & Forster 1306* (US). VENEZUELA. **Amazonas:** San Carlos de Río Negro, *Stannard 17*** (SI). **Apure:** Distrito Pedro Camejo, E side of the Galeras de Cinaruco, 6 km N of the southernmost tip, *Davidse & González 15532* (MO). **Bolívar:** along Río Sarven near Camp 9, Sarvén-tepuí, *Wurdack 34325* (G, US). **Delta Amacuro:** Ibaruma, *Tamayo 3620* (SI). **Distrito Federal:** Los Teques, *Pittier 6101* (US). **Miranda:** Dist. Páez: Fila La Tigra, Quebrada San Juan, 18 km al SO de Cúpira, *González & Ortega 1187* (MO). **Monagas:** La Pica, near Maturún, *Chase 12569* (US). **Portuguesa:** Dist. Guanare, 17 km NW of Tucupido by road, future basin of Represa Tucupido, *Davidse et al. 21503* (K, MO). **Sucre:** Península de Paria, Cerro de Río Arriba, ladera oeste del Cerro de Humo, a lo largo Río Sta. Isabel, *Steyermark 96247* (MO, US). **Táchira:** Montaña de Guafidas, just W and N of El Piñal, *Steyermark et al. 119537* (MO). **Trujillo:** along río Lora, *Pittier 10928* (US). **Yaracuy:** Distrito Nirgua, 5 km N of Nirgua by road, *Davidse et al. 20907* (MO). **Zulia:** Dist. Colón, alrededores de Casigua El Cubo, sector Las Cruces, en cerro El Mirador, *Buting & Alfonzo 7280* (MO).

13. Paspalum dispar Chase, Contr. U.S. Natl. Herb. 28(1): 96. 1929. TIPO: República Dominicana. Prov. Monte-Cristi, Cordillera Central, 100 m, 4 Jun. 1926, *E. L. Ekman H-6248* (holotipo, US-1299915!, foto SI!; isotipo, B!). Figura 16.

Plantas perennes, cespitosas, con rizomas de entrenudos cortos; *cañas* de (12–)35–90 cm de alto, 1–2 mm de diámetro, erectas, ramificadas; entrenudos de 5–15 cm de largo, aplanados, glabros, pajizos o con tintes violáceos; nudos barbados. *Vainas* más cortas que los entrenudos, aquilladas en la porción distal, papiloso-pilosas, los márgenes pestañosos; *lígulas* membranáceas, de 1 mm de largo, castañas; seudolígula ausente; cuello piloso; *láminas* lineares, de 5–30 cm de largo, 0.3–0.6 cm de ancho, planas, de base angosta y ápice agudo, pubescentes, los márgenes escabriúsculos y pestañosos. *Pedúnculos* 2–3 en la última vaina foliar, el terminal exerto, hasta de 30 cm de largo, filiforme, piloso hacia la porción distal, luego glabro, los axilares usualmente subincluidos hasta la madurez del racimo terminal. *Inflorescencias* terminales y axilares; racimo 1, arqueado; pulvínulos pilosos; raquis de los racimos de 3–7 cm de largo, 0.5–0.6 mm de ancho, triquetro, acanalado, verdoso, glabro o con los márgenes esparcidamente pilosos, terminando en una espiguilla desarrollada; pedicelos en pares, subiguales, hasta de 1.2 mm de largo, escabrosos; espiguillas irregularmente imbricadas, distribuidas en 4 series, en ocasiones la inferior abortada. *Espiguillas* anchamente elipsoides, de 1.9–2 × 1.2–1.3 mm, plano-convexas, acuminadas, pajizas a verdosas, glabras; *gluma inferior* dimorfa: triangular, con el ápice obtuso a agudo, hasta 1/3 del largo de la espiguilla, centrada, glabra, enervia, en la espiguilla superior del par; lanceolada, de ápice acuminado, 3/4–4/4 del largo de la espiguilla, excéntrica, glabra, 1-nervia, el nervio escabroso, en la espiguilla inferior; *gluma superior* 3/4 a 4/5 del largo de la espiguilla, dejando libre el dorso del antecio superior, no papilosa, (3)5-nervia, con un nervio central, los restantes submarginales, endurecidos y aquillados; *lemma inferior* tan larga como la espiguilla, cartácea, no sulcada, no papilosa, (3)5-nervia, con un nervio medio, los restantes submarginales, endurecidos y prominentes, con los márgenes doblados sobre el antecio; *pálea inferior* ausente o presente, cuando presente lanceolada, tan larga como el antecio superior, hialina; *flor inferior* ausente a estaminada o perfecta, estambres 3, anteras hasta de 0.9 mm de largo; *antecio superior* anchamente elipsoide, de 1.8–1.9 mm de largo, 1.1 mm de ancho, plano-convexo, crustáceo, pajizo, lemma y pálea con células cuadradas a rectangulares, con paredes laterales marcadamente onduladas y paredes tangenciales globosas, no papilosas, lemma con micropelos 2–5-celulares en los bordes, cuerpos de sílice escasos y elípticos; lodículas ca 0.2 mm de largo; estambres 3, anteras de 1 mm de largo. *Cariopsis* elipsoide, de 1.3 mm de largo, 0.8 mm de ancho; hilo elíptico, 1/4 del largo de la cariopsis; embrión 1/3 del largo de la cariopsis.

Número cromosómico. $2n = 20$ (Davidse & Pohl, 1972a), $2n = 40$ (Gould & Soderstrom, 1967).

Distribución y ecología. *Paspalum dispar* es endémica de la República Dominicana (Fig. 8). Ha-

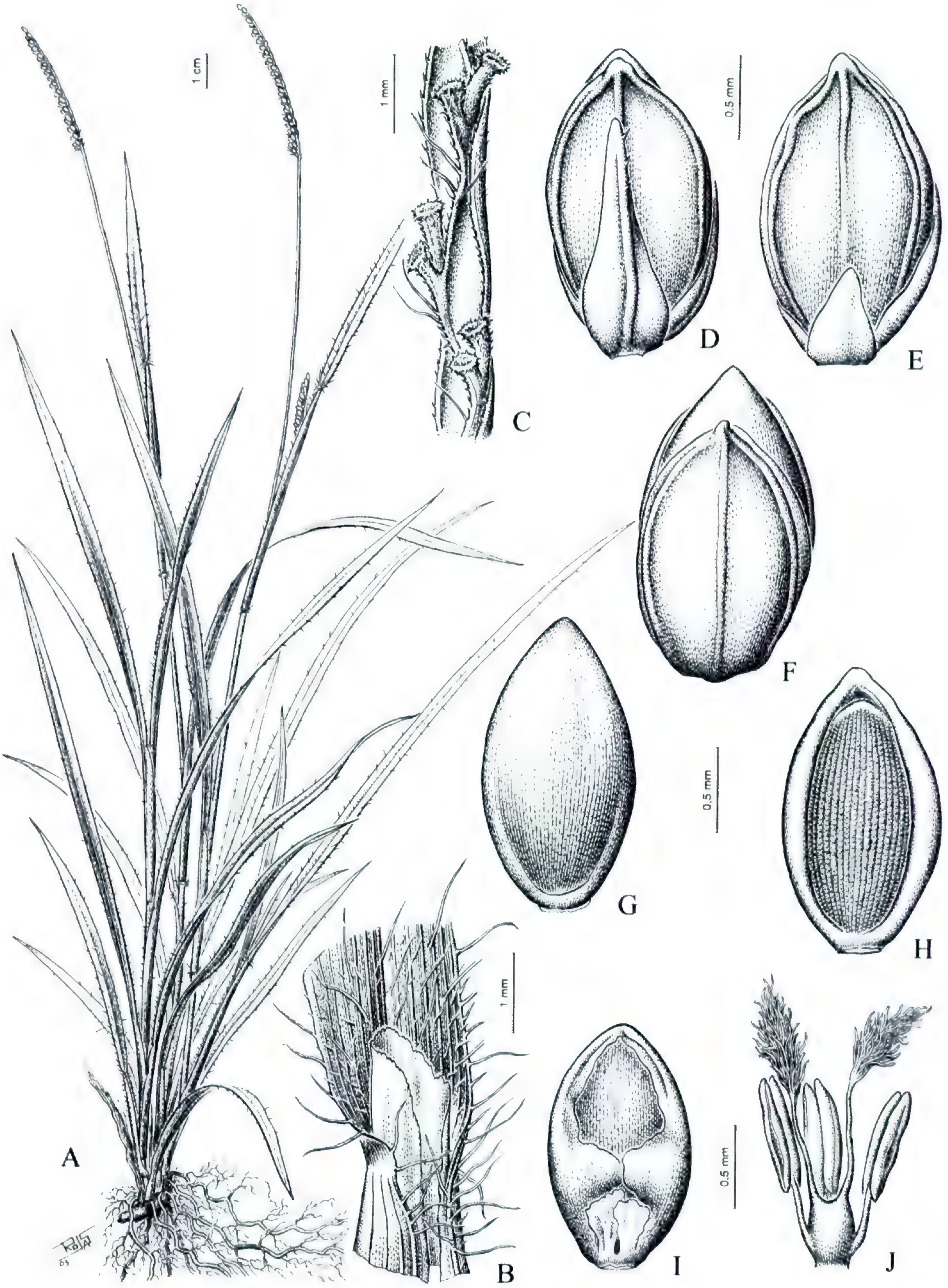

Figura 16. *Paspalum dispar.* —A. Hábito. —B. Detalle de la lígula. —C. Porción del raquis de los racimos, pedicelos. —D. Espiguilla inferior, vista ventral mostrando la gluma inferior y lemma inferior. —E. Espiguilla superior, vista ventral mostrando la gluma inferior y lemma inferior. —F. Espiguilla, vista dorsal mostrando la gluma superior. —G. Antecio superior, vista dorsal mostrando la lemma. —H. Antecio superior, vista ventral mostrando la pálea. —I. Pálea superior y lodículas. —J. Gineceo y androceo del antecio superior. (A–J, *Ekman 13426.*)

bita en bosques de pinos o en claros, en sitios húmedos, entre los 160–1600 m s.m.

Observaciones. Especie afín a *P. decumbens*; ésta última se diferencia por las cañas apoyantes, decumbentes o arraigadas en los nudos basales (vs. cañas erectas), láminas lanceoladas de 3.5–8(–10) cm de largo, 0.4–1 cm de ancho y base redondeada (vs. láminas lineares de 5–30 cm de largo, 3–6 mm de ancho y base angosta); espiguillas de 1.2–1.8 mm de largo, 1–1.1 mm de ancho, obovadas (vs. espiguillas de 1.9–2 mm de largo, 1.2–1.3 mm de ancho, anchamente elipsoides); gluma inferior que abraza la lemma inferior (vs. no abrazadora), gluma inferior de la espiguilla inferior hasta 3/4 de la espiguilla (vs. 3/4–4/4 de la espiguilla); gluma superior 1/2–3/4 del largo de la espiguilla (vs. 3/4–4/5); lemma inferior finamente papilosa (vs. no papilosa).

Material estudiado. REPÚBLICA DOMINICANA. **Azua:** sin loc., 20 Feb. 1929, *Ekman 11595* (US). **La Altagracia:** Villa Altagracia, *Ekman 11255* (US). **La Vega:** Constanza, Ciénaga de la Culata, *Liogier 15976*** (US); 18 km N of Jarabacoa, *Davidse 2626* (MO); 4 mi. S of La Vega, *Liogier 15864* (US); sin loc., 26 Oct. 1929, *Ekman 13928* (US). **Santiago:** Loma del Puerto, *Gould & Jimenez 10896* (US); sin prov., Cordillera Central, *Ekman 13426** (US).

14. Paspalum calliferum S. Denham, nom. nov. Nombre reemplazado: *Thrasya robusta* Hitchc. & Chase, Contr. U.S. Natl. Herb 18(7): 297. 1917, non *Paspalum robustum* Link ex Steud., Nomencl. Bot. 2: 273. 1841. TIPO: West Indies. Trinidad: St. Joseph, 23 Dec. 1912, *A. S. Hitchcock 10187* (holotipo, US-86559!; isotipo, K!).

Referencias. Para descripción de la especie véase Burman (1985 [1987]); ilustración en Pohl (1980).

Número cromosómico. $2n = 60$ (Pohl & Davidse, 1971).

Distribución y ecología. Burman (1985 [1987]) describe la distribución de esta especie en Trinidad y Tobago, Costa Rica, Colombia y Venezuela. Judziewicz (1990) cita a esta especie en Trinidad y Tobago y en Surinam (Fig. 17). En el presente estudio se observaron, además, ejemplares de Panamá y de Guayana Francesa. *Paspalum calliferum* crece en sabanas abiertas o en bordes de bosques, entre 500–1400 m s.m.

Observaciones. *Paspalum calliferum* se caracteriza por sus plantas de 90–150 cm de altura, los nudos barbados, racimos de 8–30 cm de largo, con el raquis foliáceo y por presentar espiguillas con un callo bien desarrollado en la base. Las espiguillas se disponen usualmente en posición "thrasyoide"; sin embargo, los especímenes *Hoock 1016* y *Davidse et al. 4754* presentan espiguillas dispuestas en posición "paspaloide."

Esta especie es afín a *P. foliiforme*; ambas especies se diferencian porque en *P. foliiforme* la gluma superior presenta el ápice acuminado, con pelos blanquecinos y rígidos, más abundantes hacia la mitad inferior, y el raquis de los racimos es más ancho, de 4–7 mm; mientras que en *P. calliferum* la gluma superior es de ápice agudo, con pelos delicados en toda la superficie y el raquis de los racimos es de 2.5–3 mm de ancho.

Burman (1985 [1987]) mantiene a ambas entidades separadas debido a que las escasas colecciones de *P. calliferum* no permiten conocer acabadamente su morfología. En el presente estudio se sigue el mismo criterio, si bien existen ejemplares que presentan caracteres conflictivos, como espiguillas con la gluma superior acuminada pero con pelos delicados en toda la superficie y medidas del largo y ancho del raquis intermedias entre ambos taxones (por ejemplo: *Davidse et al. 4754* y *Zuloaga et al. 4395*).

El epíteto específico del nombre nuevo hace referencia al callo bien desarrollado en la base de las espiguillas.

Material representativo estudiado. COSTA RICA. **Puntarenas:** San Antonio-Boruca, *Pohl & Davidse 10978* (US). GUAYANA FRANCESA. **Cayena:** sin loc., *Hoock 1016* (US). PANAMÁ. **Chiriquí:** *Davidse & D'Arcy 10137*** (MO). VENEZUELA. **Bolívar:** campamento La Ciudadela, S of El Dorado, *Davidse et al. 4754** (MEXU). **Miranda:** área metropolitana, Par. Nac. El Ávila, *Morrone et al. 4740* (SI). **Portuguesa:** Guanare, predio de la Universidad Nac. Exp. de los Llanos Centrales E. Zamora, *Morrone et al. 4694* (SI).

15. Paspalum foliiforme S. Denham, nom. nov. Nombre reemplazado: *Panicum petrosum* Trin., Sp. Gram 3: t. 280. 1831, non *Paspalum petrosum* Swallen, Phytologia 14: 362. 1967. *Tylothrasya petrosa* (Trin.) Döll, Fl. Bras. 2(2): 296, pl. 37. 1877. *Thrasya petrosa* (Trin.) Chase, Proc. Biol. Soc. Washington 24: 115. 1911. *Thrasya petrosa* (Trin.) Kuhlm., Comm. Lin. Telegr., Bot. 67 (Bot. 11): 93. 1922, comb. superfl. TIPO: Brasil. M. Cuyaba, Feb. 1827, *G. H. von Langsdorff s.n* (holotipo, LE-TRIN-0833.01!, foto SI!; isotipo, US no visto).

Panicum petrosum var. *mollis* Pilg., Bot. Jahrb. Syst. 30: 134. 1901. TIPO: Brasil. Mato Grosso: Apr. 1899, *H. Meyer 527* (holotipo, B no visto; isotipo, US no visto).

Thrasya petrosa (Trin.) Chase var. *ciliata* A. G. Burm., Brittonia 32: 220. 1980. TIPO: Brasil. Minas Gerais:

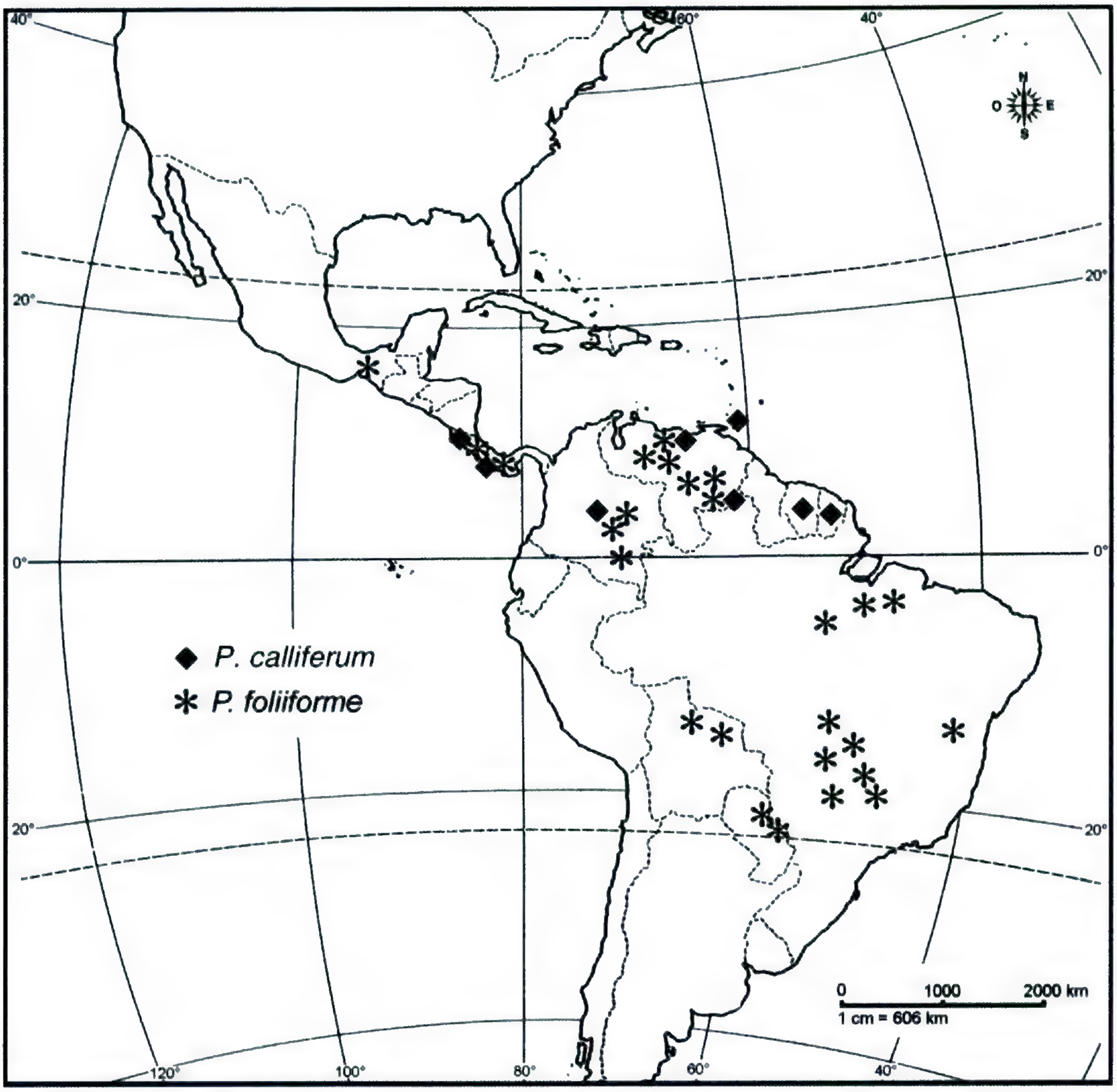

Figura 17. Distribución de *Paspalum calliferum* y *P. foliiforme*.

Mun. Diamantina, N of road from Diamantina to Curralinho, km 10, in cerrado, 11 Abr. 1979, *A. G. Burman 454* (holotipo, SP no visto; isotipo, US no visto).

Referencias. Para descripción de la especie véase Burman (1985 [1987]); ilustración en Pohl (1980).

Número cromosómico. $2n = 40$ (Pohl & Davidse, 1971).

Distribución y ecología. Paspalum foliiforme crece desde Panamá a Brasil y Paraguay; menos frecuentemente en México y en Centro América (Fig. 17). Burman (1985 [1987]) cita a la especie como dudosa en Perú. Crece en cerrados, sabanas y en áreas modificadas, desde el nivel del mar hasta los 1100 m s.m.

Observaciones. Esta especie se distingue por sus plantas hasta de 200 cm de alto, con racimos de 15–35 cm de largo, con los raquis foliáceos, comúnmente con tintes anaranjados, que cubren parte de las espiguillas (aunque a la madurez puede enrollarse a lo largo); sus espiguillas, de 3.5–6 mm de largo, presentan un callo bien desarrollado en la base, la gluma inferior se encuentra sólo en la espiguilla inferior y la gluma superior y lemma inferior son acuminadas y conspicuamente pilosas. Ver comentarios bajo *P. calliferum.*

Burman (1980) distingue a *T. petrosa* var. *ciliata,* que crece en cerrados o campos rupestres en Minas Gerais y Goiás, por presentar plantas más delicadas, hojas más cortas y angostas (3.5 mm de ancho), lígula más larga, racimos más cortos (12 cm) y suavemente ciliados y por la gluma inferior ciliada. Si bien no se localizaron los ejemplares citados por Burman bajo esta variedad, la misma no es aquí

aceptada ya que entre los ejemplares estudiados se observa un continuo en el ancho de las hojas y el largo de los racimos. Por otra parte, Burman (1985 [1987]) menciona que esta especie es variable en su morfología y que plantas de poca altura (30 cm) pueden florecer si bien el tamaño normal de las plantas es de 100–150 cm.

El colector del ejemplar tipo de *Panicum petrosum* es dudoso; si bien Chase (1911) menciona que el ejemplar con el labelo "m. Cuyaba, Feb. 1827" en el herbario de Trinius, fue probablemete coleccionado por G. H. von Langsdorff, existe un ejemplar *Riedel s.n.* en K que probablemente sea un isotipo. Véase Renvoize (1978) para comentarios de las colecciones de Langsdorff y Riedel.

El epíteto específico del nombre nuevo hace referencia al raquis foliáceo.

Material representativo estudiado. BRASIL. **Acre:** Río Branco, *Rondon s.n.* (US). **Bahía:** Mucugé, *Zuloaga et al. 4793* (SI). **Distrito Federal:** *Clayton 4868a* (US). **Goiás:** São João de Aliança, *Filgueiras & Zuloaga 2052* (SI). **Maranhão:** Carolina, *Swallen 3873* (US). **Mato Grosso:** Barra do Garcas, *Anderson 9774*/*** (US). **Pará:** Alto Tapajos, *Anderson 10782* (US). COLOMBIA. **Guaviare:** San José del Guaviare, *Giraldo-Cañas & López 2594* (SI). **Meta:** ruta de San Martín a Granada, *Zuloaga 3991* (SI). COSTA RICA. **Puntarenas:** 7 km SW of río Catarata, *Riggins 678* (MEXU). MÉXICO. **Chiapas:** Ocosingo, *Martínez et al. 25239* (MEXU). PARAGUAY. **Amambay:** Par. Nac. Cerro Corá, *Morrone & Pensiero 524* (SI). VENEZUELA. **Aragua:** Placibel, vía Colonia Tovar por La Victoria, sector Loma Briza, *Morrone et al. 4669* (SI). **Bolívar:** San Ignacio de Yuraní, *Zuloaga et al. 4414* (SI). **Miranda:** Los Teques, *Burkart 16291* (SI). **Portuguesa:** Acarigua, *Burkart 17079* (SI).

16. Paspalum glaziovii (A. G. Burm.) S. Denham, comb. nov. Basónimo: *Thrasya glaziovii* A. G. Burm., Brittonia 34: 460. 1982. TIPO: Brasil. Goiás: Sto. Antônio do Descoberto, campo rupestre, ca. 5 km da cidade, 27 Mar. 1980, *T. S. Filgueiras 694* (holotipo, IBGE no visto; isotipos, BR!, foto SI!, K no visto, SP no visto, UB no visto, US no visto).

Referencias. Para descripción e ilustración de la especie véanse protólogo y Burman (1985 [1987]).

Distribución y ecología. Esta especie es frecuente en los cerrados del centro de Brasil, en Mato Grosso (Burman, 1985 [1987]), Distrito Federal y Goiás; se suma una colección de Bolívar, Venezuela (Fig. 6).

Observaciones. *Paspalum glaziovii* se distingue por los racimos solitarios, de 8–13 cm de largo, el raquis de los racimos es foliáceo, de 3–4 mm de ancho, pajizo o ferrugíneo, con pelos papilosos en los márgenes y frecuentemente pelos adpresos y pajizos en la superficie, las cañas son delgadas y ferrugíneas. También se diferencia en las espiguillas, de 2.7–3.5 mm de largo, con un callo en la base, además no se desarrolla la gluma inferior.

Material estudiado. BRASIL. **Distrito Federal:** Lago Norte, *Filgueiras & Zuloaga 2193*** (SI); sin localidad, *Irwin et al. 15348** (US). **Goiás:** *Glaziou 22433* (US); sin loc., 7 May 1895, *Glaziou 22483* (US). VENEZUELA. **Bolívar:** Gran Sabana, Par. Nac. Canaima, 22 km de Kama-meru, camino a Santa Elena, *Morrone et al. 4776* (SI).

17. Paspalum graniticum (A. G. Burm.) S. Denham, comb. nov. Basónimo: *Thrasya granitica* A. G. Burm., Brittonia 32: 219. 1980. TIPO: Surinam. Voltzberg, 1953–1954, *J. P. Schultz 7783* (holotipo, BBS no visto; isotipos, U no visto, US-2902701!, foto SI!).

Referencias. Para descripción e ilustración de la especie véanse protólogo y Burman (1985 [1987]).

Distribución y ecología. Especie endémica de Surinam, crece principalmente sobre afloramientos rocosos (Fig. 12).

Observaciones. Se conocen escasas colecciones de *Paspalum graniticum.* Esta especie presenta inflorescencias con 1–4 racimos, terminandos en una espiguilla desarrollada; el raquis es angosto (0.9–1.1 mm) y usualmente glabro; las espiguillas son glabras, de 2.4–2.6 mm de largo y hasta de 0.7 mm de ancho. Se observaron papilas simples y escasos cuerpos de sílice en el antecio.

Material estudiado. SURINAM. Voltzberg, Coppename River, *Schulz & Donselaar 10581*/*** (US); Voltzberg, *Schulz & Donselaar 10617* (US paratipo).

18. Paspalum hintonii Chase, J. Washington Acad. Sci. 27: 143. 1937. TIPO: México. Temascaltepec: Vigas, 1080 m, 22 Sep. 1932, *G. B. Hinton 1807* (holotipo, US-1611719!, foto SI!; isotipos, MO!, TEX no visto). Figura 18.

Plantas perennes, cespitosas, con rizomas de entrenudos cortos; *cañas* de 30–90 cm de alto, 2–3 mm de diámetro, erectas a apoyantes, delicadas, ramificadas en los nudos basales; entrenudos comprimidos, de 5–25 cm de largo, estriados, glabros; nudos glabros a pilosos, castaños, angulosos. *Vainas* de 4–15 cm de largo, estriadas, glabras, márgenes densamente pestañososo glabros; *lígulas* membranáceas, de 0.8–1.5 mm de largo, con el ápice recto; seudolígula con pelos hasta de 4 mm de largo; cuello piloso; *láminas* lineares, de 6–28 cm de largo, 0.3–0.7(–0.9) cm de ancho, planas, de base atenuada, raro redondeada y ápice acuminado, glabras

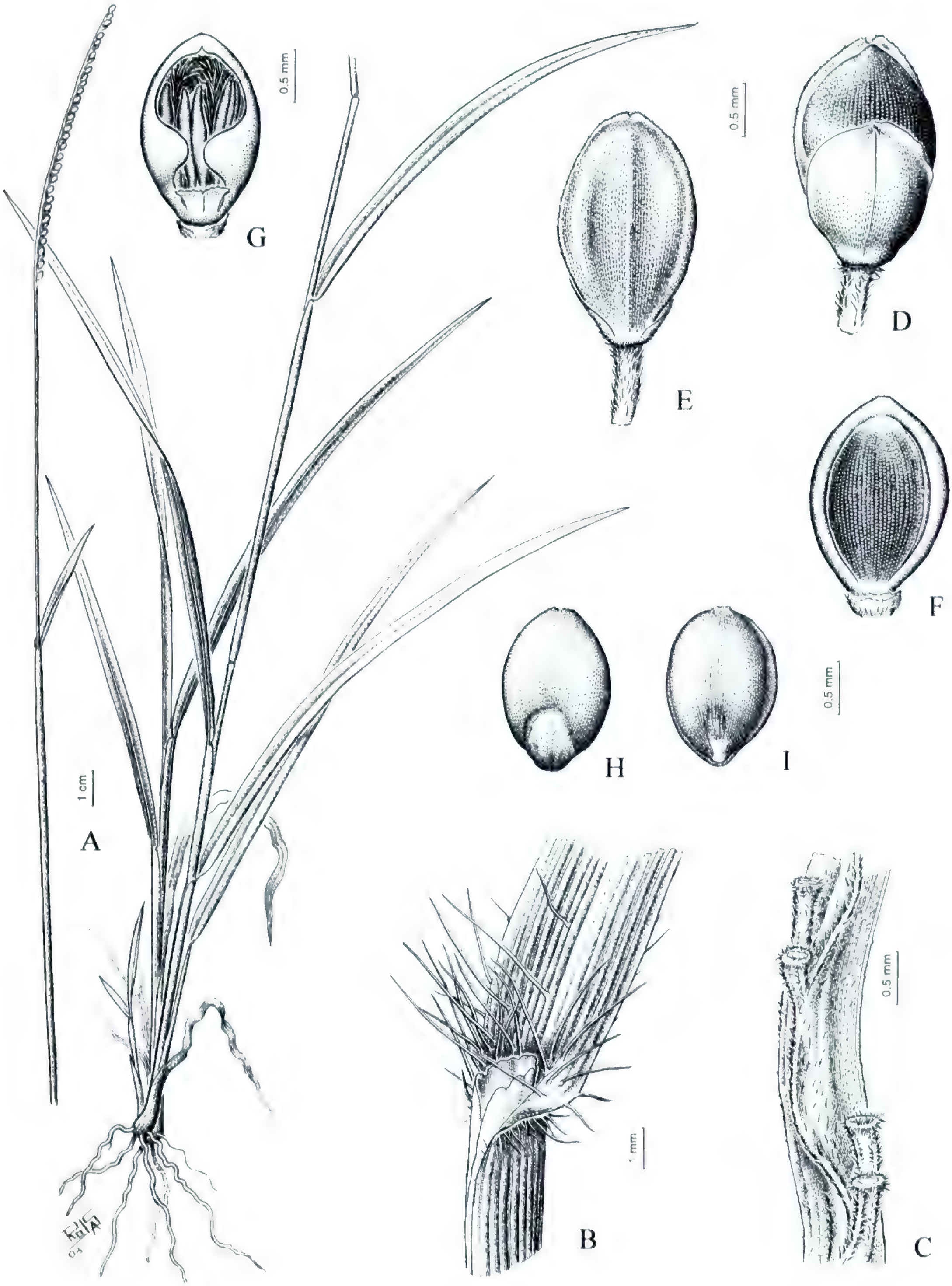

Figura 18. *Paspalum hintonii.* —A. Hábito. —B. Detalle de la lígula. —C. Porción del raquis de los racimos, pedicelos. —D. Espiguilla, vista dorsal mostrando la gluma superior. —E. Espiguilla, vista ventral mostrando la lemma inferior. —F. Antecio superior, vista ventral mostrando la pálea. —G. Pálea superior, lodículas, estambres y estigma. —H. Cariopsis, mostrando el embrión. —I. Cariopsis, mostrando el hilo. (A–I. *McVaugh 19109.*)

a pubescentes, los márgenes escabrosos, en ocasiones con pelos tuberculados, el nervio medio marcado o aquillado. *Pedúnculos* 1–3(4) en la última vaina foliar, generalmente uno de ellos incluido, los restantes exertos, hasta de 40 cm de largo, de 0.3–0.5 mm de diámetro, filiformes, glabros a cortamente pilosos hacia el ápice; ocasionalmente con pedúnculos presentes en las vainas subapicales. *Inflorescencias* terminales y axilares; racimo 1, ascendente, recto a levemente arqueado; pulvínulos pilosos; raquis de los racimos de 4–11 cm de largo, 0.7–1 mm de ancho, triquetro, acanalado, glabro, terminando en una espiguilla desarrollada; pedicelos en pares, hispídulos, desiguales, el de la espiguilla superior hasta de 1.1 mm de largo; espiguillas imbricadas, dispuestas en 2–4 series sobre el raquis. *Espiguillas* anchamente elipsoides a ligeramente obovoides, de 2–2.4(–3) mm de largo, 1–1.3 mm de ancho, plano-convexas a ligeramente cóncavo-convexas, pajizas o con tintes violáceos, glabras; *gluma inferior* ausente, ocasionalmente presente en alguna espiguilla inferior o superior del par, escamosa, menor a 1/6 del largo de la espiguilla, centrada, glabra, enervia; *gluma superior* 1/2 del largo de la espiguilla, más angosta que la espiguilla, dejando al descubierto gran parte del antecio, papirácea, finamente papilosa, glabra, 3(5)-nervia, cuando 5-nervia, los nervios marginales próximos entre sí; *lemma inferior* tan larga como la espiguilla, cartácea, plana a ligeramente cóncava, no sulcada, fuertemente papilosa, glabra, 3(5)-nervia, el nervio central tenue y los laterales prominentes, endurecidos, verdes, cuando 5-nervia los nervios marginales próximos entre sí, los márgenes doblados sobre el antecio; *pálea inferior* ausente o tan larga como la lemma, hialina; flor inferior ausente o estaminada, estambres 3, anteras de 1.2 mm de largo; *antecio superior* anchamente elipsoide a obovoide, de 2.2–2.4 mm de largo, 1.3–1.4 mm de ancho, crustáceo, plano-convexo, pajizo, lemma y pálea con células cuadradas, de paredes onduladas, con papilas verrugosas regularmente distribuidas, centradas en las células, con 5–6 verrugas cada una, micropelos en el ápice de la pálea y ápice y bordes de la lemma, con la célula apical dos veces más larga que la basal; lemma con un mechón apical de macropelos unicelulares; lodículas de 0.3–0.4 mm de largo; estambres 3, anteras de 1.2 mm de largo, purpúreas. *Cariopsis* subcircular a elipsoide, 1.4–1.6 mm de largo, 0.8–1 mm de ancho; hilo elíptico, 1/4–1/3 de la cariopsis; embrión 1/3–1/2 de la cariopsis.

Distribución y ecología. *Paspalum hintonii* es endémica de México, encontrándose en los estados de Jalisco, México, Nayarit y Oaxaca (Fig. 19); es frecuente en los bosques de pino y encino y en selvas, sobre suelos arcillosos, rojos o volcánicos; ha sido colectada en cafetales o cultivos de maíz, en áreas perturbadas y bordes de caminos, entre 100–1900 m de altura. Especie forrajera (Mejía Saulés & Dávila Aranda, 1992).

Observaciones. *Paspalum hintonii* se diferencia de las restantes especies del grupo Decumbentes por sus espiguillas usualmente sin la gluma inferior, la gluma superior hasta de 1/2 de la espiguilla y más angosta que ésta, finamente papilosa y la lemma inferior fuertemente papilosa, con los nervios laterales prominentes. Las cañas son delicadas, delgadas y los racimos solitarios de 4–11 cm de largo.

El ejemplar *Reeder & Reeder 2414* presenta la lemma inferior no papilosa y la gluma superior algo mayor a 1/2 de la espiguilla, pero más angosta que ésta. El ejemplar tipo de *P. hintonii* presenta espiguillas en el límite inferior del tamaño frecuente para la especie, de 2 mm de largo y 1 mm de ancho.

Material representativo estudiado. MÉXICO. **Jalisco:** 11–12 mi. S of Talpa de Allende, *McVaugh 20246*** (US). **México:** Tejumilco, al NW del pueblo, *Vibrans 5427* (MEXU). **Nayarit:** 8 mi. NE of Tepic, *Reeder & Reeder 2414* (MEXU). **Oaxaca:** Pochutla, San Miguel del Puerto, *Rivera et al. 1788* (MEXU).

19. Paspalum huberi S. Denham, nom. nov. Nombre reemplazado: *Thrasya stricta* A. G. Burm., Acta Bot. Venez. 14(4): 75, f. 16. 1985 [1987], non *Paspalum strictum* Pers., Syn. Pl. 1: 86. 1805. TIPO: Venezuela. Amazonas: "terreno situado entre la carretera hacia Sanariapo y la pista de aterrizaje del aeropuerto de Puerto Ayacucho", 21 Ago. 1977, *O. Huber 974* (holotipo, MO-2806206 no visto; isotipos, US-3107016!, VEN no visto).

Referencias. Para descripción de la especie véase protólogo.

Distribución y ecología. Hasta el presente esta especie se conocía sólo para la región de Ayacucho en Venezuela; en el presente trabajo se agrega una colección para Colombia, en el estado de Meta (Fig. 12).

Observaciones. *Paspalum huberi* presenta cañas delgadas y muy ramificadas, los raquis de los racimos son foliáceos y glabros; las espiguillas presentan un callo en la base, la gluma superior es 1/2 del largo de la espiguilla y más angosta que ésta, glabra y acuminada.

El epíteto específico del nombre nuevo hace referencia al colector del ejemplar tipo.

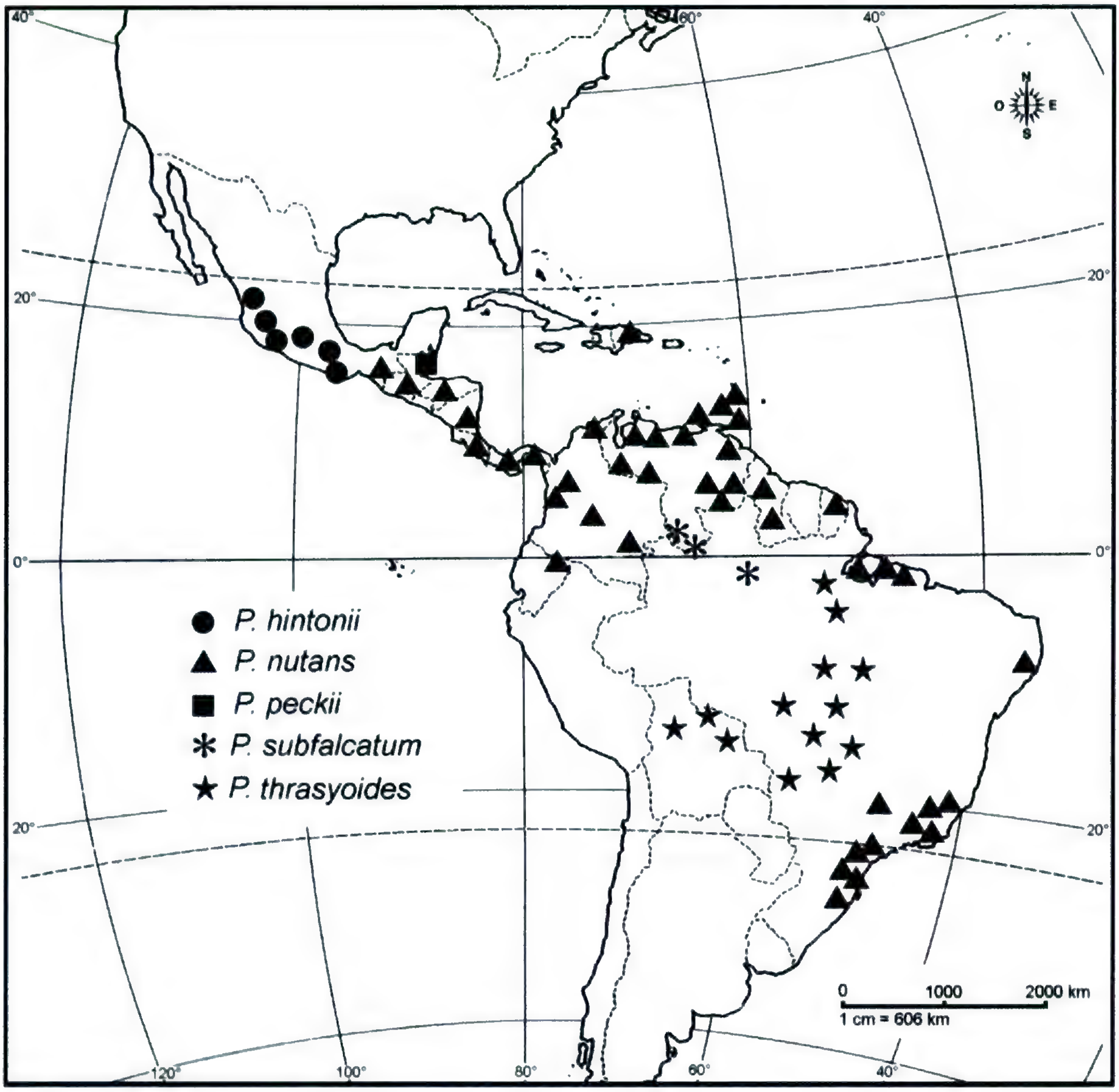

Figura 19. Distribución de *Paspalum hintonii, P. nutans, P. peckii, P. subfalcatum* y *P. thrasyoides.*

Material estudiado. COLOMBIA. **Meta:** along rd. to Hac. Rubiales, *Laegaard & Mayorga* 17572 (SI).

20. Paspalum inconstans Chase, Contr. U.S. Natl. Herb. 24(8): 446. 1927. TIPO: Bolivia. Hacienda Casana, on rd. to Tipuani, 1400 m, 19 Nov. 1922, *O. Buchtien 7107* (holotipo, US-1164822!, foto SI!; isotipo, MO-941377!). Figura 20.

Paspalum lepidum Chase, Contr. U.S. Natl. Herb. 24(8): 447. 1927. TIPO: Bolivia. Coroico, Nor-Yungas, 1560 m, 25 Dec. 1923, *A. S. Hitchcock 22726* (holotipo, US-1164799!, foto SI!).

Plantas perennes, cespitosas o con rizomas plagiótropos; *cañas* de 20–90 cm alto, 2–3 mm de diámetro, erectas a geniculadas en los nudos basales, ramificadas en los nudos basales y medios; entrenudos de 5–12 cm de largo, finamente estriados, glabros; nudos comprimidos, castaños, glabros a pilosos. *Vainas* de 3–11 cm de largo, usualmente más cortas que los entrenudos, las basales comúnmente pilosas, flojas, aquilladas, las superiores glabrescentes a pubescentes, los márgenes pestañosos; *lígulas* membranáceas, de 1–2.5 mm de largo, castañas; seudolígula presente, con pelos hasta de 3.5 mm de largo; cuello densamente piloso; *láminas* lineares a linear-lanceoladas, de 7–25 cm de largo, 0.5–1.3 cm de ancho, las inferiores planas a plegadas, de base corta a largamente atenuada y ápice acuminado, glabras a cortamente híspidas o vilosas en ambas caras, los márgenes pestañosos. *Pedúnculos* 1–2(4) en la última vaina foliar, subincluidos a exertos, hasta de 30 cm de largo, generalmente glabros a cortamente pubescentes; ocasionalmente presentes en las vainas subapicales. *Inflorescencias* terminales y axilares; racimos 1–4(9), alternos, ar-

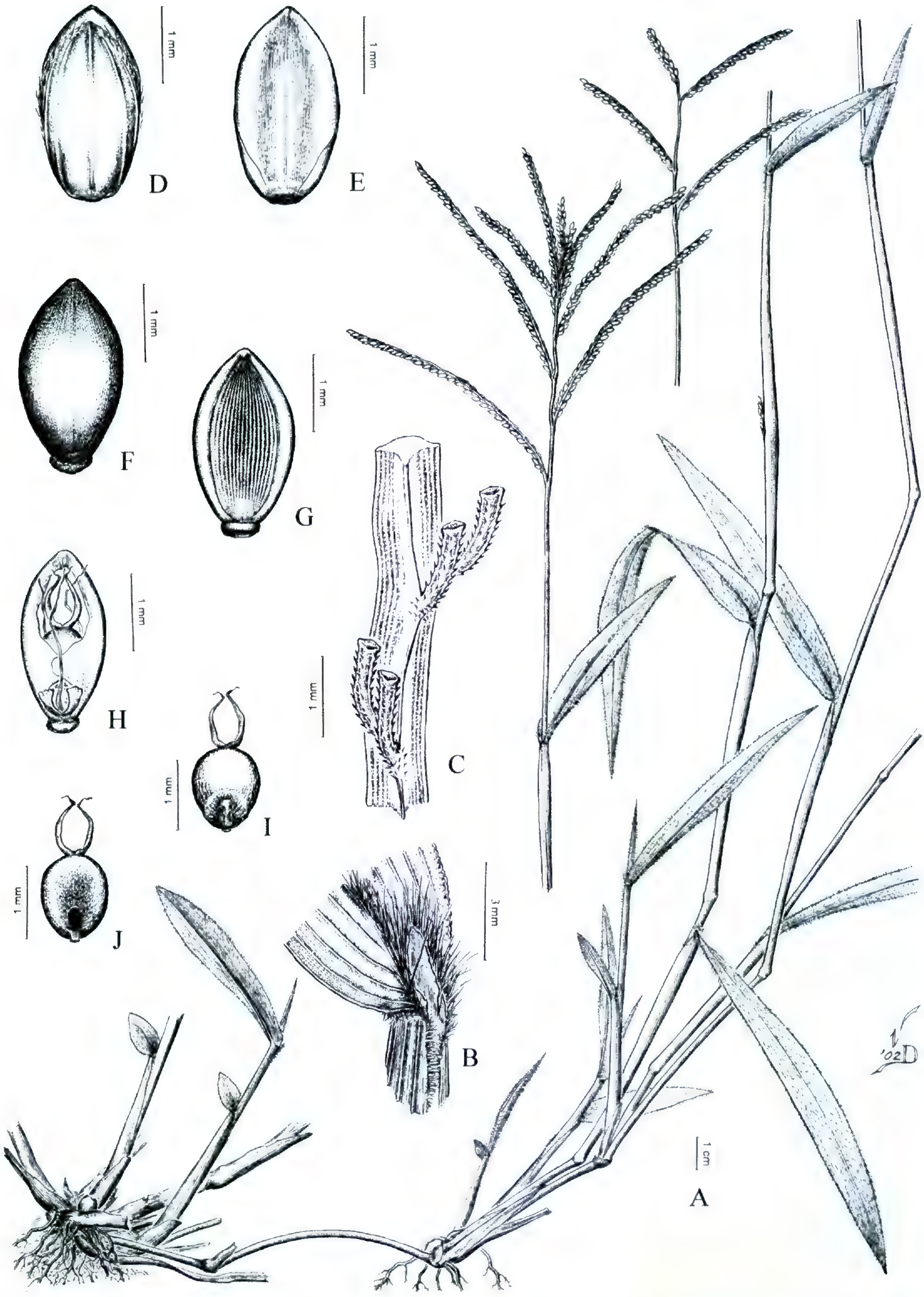

Figura 20. *Paspalum inconstans.* —A. Hábito. —B. Detalle de la lígula. —C. Porción del raquis de los racimos, pedicelos. —D. Espiguilla, vista dorsal mostrando la gluma superior. —E. Espiguilla, vista ventral mostrando la lemma inferior. —F. Antecio superior, vista dorsal mostrando la lemma. —G. Antecio superior, vista ventral mostrando la pálea. —H. Pálea superior, lodículas y cariopsis. —I. Cariopsis, mostrando el embrión. —J. Cariopsis, mostrando el hilo. (A–J, *von Sneidern 159* y *Hitchcock 22734.*)

queados o rectos, divergentes; eje principal de 3–6 cm de largo, aplanado, glabro; pulvínulos cortamente pilosos; raquis de los racimos de 3–8(–11) cm de largo, 0.6–0.8(–1.5) mm de ancho, triquetro, glabro a hispídulo en la cara abaxial, con los márgenes lisos a escabriúsculos, terminando en una espiguilla desarrollada; pedicelos en pares, desiguales, el de la espiguilla superior de 1–2 mm de largo, hispídulos; espiguillas imbricadas a laxamente distribuidas en 2–4 series irregulares. *Espiguillas* largamente elipsoides, de 2.2–3 mm de largo, (1–)1.2–1.3 mm de ancho, plano-convexas a levemente cóncavo-convexas, de ápice agudo a levemente obtuso, verdosas, pálidas o con tintes violáceos, glabras a cortamente cilioladas; *gluma inferior* comúnmente ausente, cuando presente frecuente en la espiguilla inferior del par, rudimentaria, ancha y de ápice obtuso, hasta 1/6 del largo de la espiguilla, raro lanceolada y hasta 2/3 del largo de la espiguilla, centrada o excéntrica, glabra o con los márgenes cortamente ciliolados, enervia o 1-nervia; *gluma superior* usualmente más corta que la espiguilla, dejando libre el ápice del antecio superior, membranácea a papirácea, no papilosa, con los márgenes cortamente ciliolados, con pelos delicados hasta de 0.3 mm de largo, el resto de la superficie glabra o con unos pocos pelos adpresos, a veces totalmente glabra, 5-nervia, con un nervio central, los restantes marginales, próximos entre sí; *lemma inferior* tan larga como la espiguilla, cartácea, con células alargadas y de paredes marcadas, no papilosa, no sulcada a levemente sulcada, glabra, 5-nervia, con un nervio central y los restantes marginales, próximos entre sí, con los márgenes doblados sobre el antecio; *pálea inferior* más angosta y tan larga o más corta que la lemma, hialina; *flor inferior* ausente o estaminada; estambres 3, anteras de 1 mm de largo; *antecio superior* elipsoide, de 2–2.7 mm de largo, 1 mm de ancho, plano-convexo, crustáceo, pajizo; lemma y pálea con células cuadradas, de paredes onduladas, con papilas verrugosas, distribuidas regularmente en toda su superficie, centradas en las células, con 2 verrugas cada una, micropelos bicelulares hacia la porción superior de lemma y pálea; lodículas ca. 0.2 mm de largo; estambres 3, anteras ca. 1 mm de largo. *Cariopsis* elipsoide, de 1.3–1.4 mm de largo, 0.8–1 mm de ancho; hilo elíptico, 1/4–1/3 de la cariopsis; embrión 1/3–1/2 de la cariopsis.

Distribución y ecología. Crece en Colombia, Ecuador, Perú y Bolivia; en esta contribución se agregan colecciones de Venezuela (Fig. 11); habita en bosques nublados y campos abiertos, en lugares sombreados, en los márgenes de ríos, en suelos húmedos o rocosos, también crece en áreas perturbadas y bordes de caminos, entre 800–3200 metros de altura. El ejemplar *Smith & Reitz 9659* (US) coincide con las características morfológicas de la especie pero su lugar de colección, Brasil, Santa Catarina, es dudoso y posiblemente corresponda a un error en la etiqueta.

Observaciones. Esta especie se distingue por presentar rizomas usualmente plagiótropos con cañas geniculadas, 1–4(9) racimos en la inflorescencia terminal, espiguillas largamente elipsoides, con la gluma superior glabra o escasamente pilosa en la superficie y delicadamente ciliolada hacia los márgenes, más corta que la espiguilla; la presencia de gluma inferior es variable: usualmente es ausente en ambas espiguillas del par o presente en la espiguilla inferior del par y ausente en la superior.

Paspalum inconstans es afín a *P. nutans* por la distribución de la gluma inferior y las espiguillas glabras a cilioladas. Se diferencian por el tamaño y la forma de las espiguillas (anchamente elipsoides a obovadas, de 1.6–2.1 mm de largo en *P. nutans* y largamente elipsoides, de 2.2–3 mm de largo en *P. inconstans*). *Paspalum inconstans* se separa de *P. botterii* por las espiguillas largamente elipsoides, usualmente glabras en la superficie y cilioladas en los márgenes, no maculadas ni con manchas glandulares.

En el ejemplar *Asplund 10623* se observaron racimos de 11 cm de largo y raquis de 1.5 mm de ancho, mientras que en *Hitchcock 22734* se observaron 9 racimos.

Paspalum inconstans y *P. lepidum* fueron descriptas para Bolivia y Ecuador por Chase (1927). Chase separa a *P. inconstans* por tener cañas de 45–85 cm de alto y hojas pubescentes a glabrescentes, mientras que *P. lepidum* presenta, de acuerdo a su criterio, cañas de 20–45 cm de alto y hojas aterciopeladas, densamente pubescentes en ambas caras. Por otra parte, esta autora señala que *P. lepidum* también se distingue por sus plantas densamente cespitosas, por sus cañas más cortas, simples y de pocos nudos. Renvoize (1998) mantiene separadas a ambas entidades distinguiendo a *P. lepidum* por sus plantas cespitosas y a *P. inconstans* por sus plantas no cespitosas, con cañas ascendentes. Del análisis del material observado, incluido el material tipo de ambas especies, se puede concluir que los caracteres usados por Chase y por Renvoize no permiten separar a las especies, debido a que existen ejemplares con condiciones intermedias en cuanto a la pilosidad de las hojas y el hábito; y el alto de las cañas es un carácter continuo. Así, el ejemplar de herbario *Cuatrecasas 22549* es una

planta de cañas decumbentes, de 30 cm de alto y con hojas aterciopeladas. En *von Sneidern 159* se observan cañas apoyantes, la porción erecta de 70 cm de altura y las láminas densamente pilosas. El ejemplar *Killip & Smith 15143* es una mata cespitosa densa, con cañas hasta de 30 cm de alto pero sus láminas son glabras. El espécimen *Bristol 967* posee cañas de 25 cm de altura, con pocos nudos (2) pero láminas no aterciopeladas. Finalmente, el ejemplar *Buchtien 7109*, determinado por Chase como *P. inconstans*, es una planta no cespitosa, alcanza 90 cm de altura y las hojas son aterciopeladas. Consecuentemente, se considera a *P. lepidum* Chase como sinónimo de *P. inconstans*.

Material representativo estudiado. BOLIVIA. **Cochabamba:** Chapre, ca. 4 km along Corani Pampa rd. from Chapare–Cochabamba, *Wood 10200* (LPB). **La Paz:** Nord Yungas, San José, *Hitchcock 22734* (US). Hacienda Casana, *Buchtien 7109* (MO, US). COLOMBIA. **Antioquia:** Camino Real Antiguo al Boquerón de Medellín, *Barkley et al. 130** (US). **Boyacá:** valley of río Pomera, *Fassett 25602* (US). **Cauca:** Chisquio, *Asplund 10623* (US). **Valle del Cauca:** El Tambo, *von Sneidern 159*** (G, US); N de Las Brisas, *Cuatrecasas 22549* (US). **Putumayo:** Valle del Sibundoy, *Bristol 967* (US). **Santander:** Mesa de los Santos, *Killip & Smith 15143* (US). ECUADOR. **El Oro:** betw. La Chorita and Portovelo, *Hitchcock 21204* (US). **Loja:** 10 km S of Loja on rd. to Zumba, then 1–2 km E on rd. to Par. Nac. Podocarpus, *Peterson & Judziewicz 9386* (MO). PERÚ. **Cuzco:** Convención, *Marin 1241* (US). VENEZUELA. **Táchira:** Camino a La Agrita y Mérida, 78 km N de San Cristóbal, 8 km antes de La Portuguesa, *Morrone et al. 4715* (SI). **Trujillo:** 1–4 km de la Peña camino a Humocaro Bajo vía Barquisemento, Quebrada de Porras, *Morrone et al. 4734* (SI).

21. Paspalum monostachyum Vasey, Fl. South. U.S. ed. 2. 665. 1883. *Paspalum rectum* var. *longispicatum* Vasey, Bot. Gaz. 9: 54, 55. 1884. TIPO: E.U.A. Florida: Miami, July 1877, *A. P. Garber 224* (holotipo, US-2855820!). Figura 21.

Plantas perennes, rizomatosas, con rizomas de entrenudos alargados, arqueados, cubiertos por catáfilos glabros; *cañas* de 50–120 cm de alto, 2–3 mm de diámetro, erectas, simples, en grupos de 1–4 cañas floríferas; entrenudos de 11–16 cm de largo, estriados, glabros; nudos glabros, pajizos o castaños. *Vainas* de 6–18 cm de largo, superpuestas hacia la base, glabras, los márgenes lisos, a amplios y pilosos hacia la zona ligular; *lígulas* membranáceas, de 1–1.5 mm de largo; seudolígula formada por escasos pelos de 2–4 mm de largo; cuello glabro; *láminas* filiformes, de 15–68 cm de largo, 1–2 mm de ancho, macizas, de base atenuada y ápice agudo, glabras. *Pedúnculos* 1, raro 2, en la última vaina foliar, exertos a subincluidos, hasta de 35 cm de largo, cilíndrico-acanalados, glabros. *Inflorescencias* terminales y axilares; racimo 1, raro 2, ligeramente arqueados a rectos; eje principal ausente o hasta de 2 cm de largo, aplanado o cilíndrico, ciliado; pulvínulos glabros a pilosos; raquis de los racimos de 10–30 cm de largo, 0.6–0.7 mm de ancho, triquetro o terete, con los márgenes escabrosos y largamente ciliados o con aguijones, terminando en una espiguilla desarrollada; pedicelos en pares, subiguales, de 0.5–1 mm de largo, escabrosos, glabros o largamente ciliados; espiguillas imbricadas, dispuestas en 4 series, en ocasiones la inferior abortada. *Espiguillas* elipsoides, de 3–3.1 mm de largo, 1.6–2 mm de ancho, plano-convexas, pajizas, glabras; *gluma inferior* ausente, raro presente en la espiguilla superior del par, vestigial o 1/3–2/3 del largo de la espiguilla, de base ancha y ápice obtuso, glabra, excéntrica, enervia; *gluma superior* ligeramente más corta que la espiguilla, dejando al descubierto el dorso del antecio, no papilosa, delicada, 3-nervia; *lemma inferior* tan larga como la espiguilla, cartácea, no sulcada, con células alargadas y de paredes marcadas, no papilosa, delicada, 3–5-nervia, cuando 5-nervia, con un nervio central y los restantes marginales, próximos entre sí, con los márgenes doblados sobre el antecio; *pálea* y flor inferior ausentes; *antecio superior* elipsoide, de 2.9–3 mm de largo, 1.5–1.6 mm de ancho, plano-convexo, crustáceo, pajizo; lemma y pálea con células rectangulares, de paredes onduladas, no papilosas, con micropelos bicelulares hacia el ápice de lemma y pálea, con la célula apical de igual largo que la basal o 1.5 veces más larga, cuerpos de sílice elípticos hacia el ápice de lemma y pálea; lodículas de 0.2–0.3 mm de largo; estambres 3, anteras de 1.2–1.3 mm de largo. *Cariopsis* elipsoide, de 1.6 mm de largo, 1.2 mm de ancho; hilo elíptico, 1/3 de la cariopsis; embrión 1/3–1/2 de la cariopsis.

Distribución y ecología. Habita en Estados Unidos de América, en los estados de Texas, Louisiana y Florida (Fig. 10); crece sobre suelos arenosos y en áreas perturbadas. Beetle et al. (1999) citan a *P. monostachyum* para México, sobre la costa del Golfo de México, en dunas costeras, entre 0–10 m s.m., aunque en este estudio no se observaron especímenes de este país.

Observaciones. *Paspalum monostachyum* se caracteriza por sus rizomas de entrenudos alargados, arqueados, láminas filiformes y macizas, racimos 1, raro 2, raquis de los racimos triquetro a terete, espiguillas glabras, sobre pedicelos largamente ciliados. La gluma inferior, cuando presente, se desarrolla en la espiguilla superior del par, en

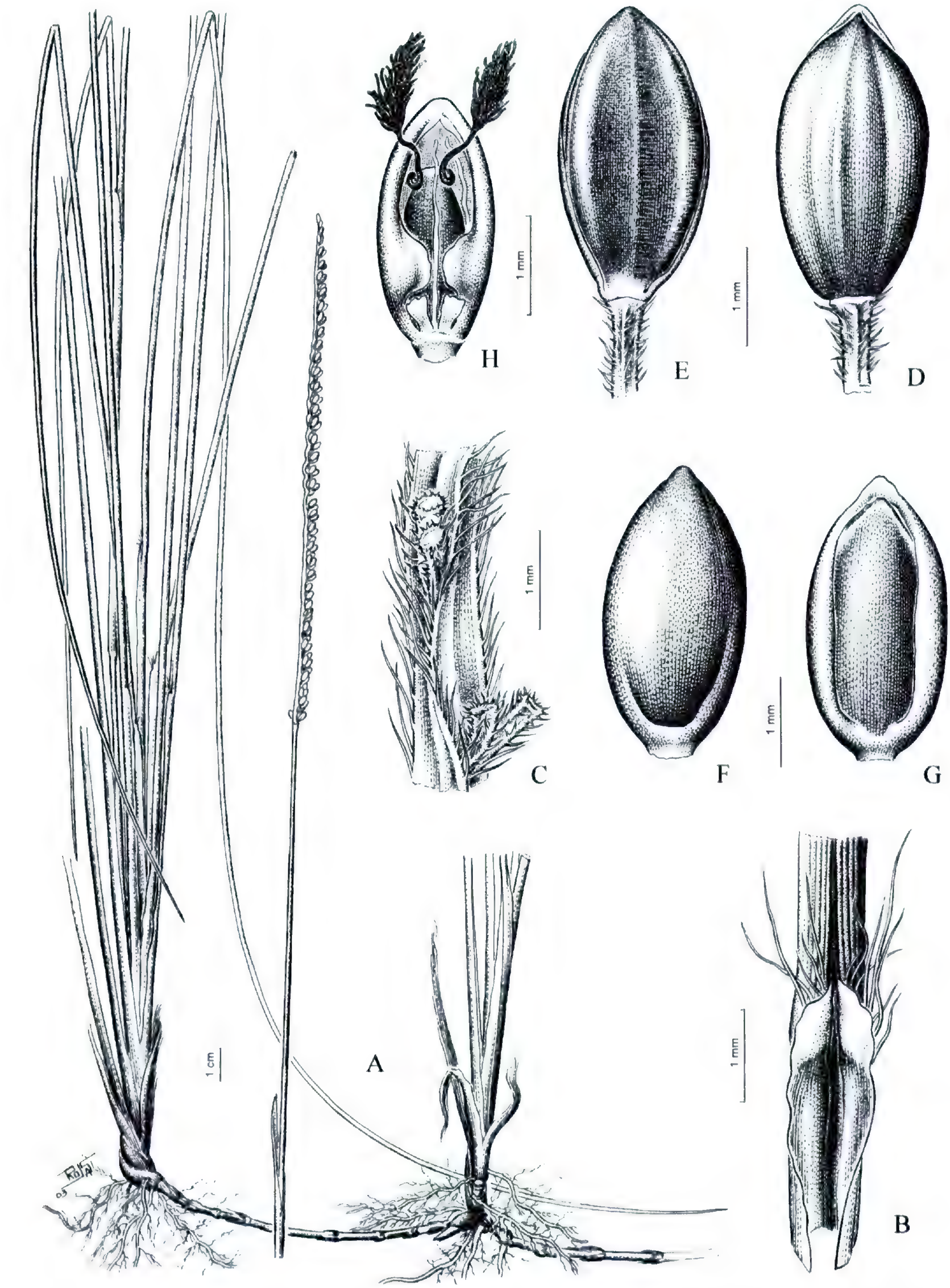

Figura 21. *Paspalum monostachyum.* —A. Hábito. —B. Detalle de la lígula. —C. Porción del raquis de los racimos, pedicelos. —D. Espiguilla, vista dorsal mostrando la gluma superior. —E. Espiguilla, vista ventral mostrando la lemma inferior. —F. Antecio superior, vista dorsal mostrando la lemma. —G. Antecio superior, vista ventral mostrando la pálea. —H. Pálea superior, lodículas y cariopsis. (A–H, *Lundell & Lundell 14704.*)

lugar de en la inferior, como ocurre en la mayoría de las restantes especies del grupo.

Esta especie es afín a *P. unispicatum*, por compartir la presencia de rizomas de entrenudos alargados, arqueados y cubiertos por catáfilos, cañas simples y racimos usualmente solitarios, largos, hasta de 18 cm en *P. unispicatum* y 30 cm en *P. monostachyum*.

Paspalum monostachyum y *P. unispicatum* se diferencian principalmente por las láminas linear-lanceoladas, planas a plegadas en *P. unispicatum*. Por otra parte, la distribución de *P. monostachyum* es más restringida, en el sur de Estados Unidos de América, mientras que *P. unispicatum* crece desde México y Centro América hasta Argentina y Uruguay.

Material estudiado. ESTADOS UNIDOS DE AMÉRICA. **Florida:** Paradise Key, *Mosier 250* (US); Collier, 8 mi. E of Naples, *Cooley et al. 9055* (US). **Louisiana:** beach ridge, Jhonson Bagon, Cameron Parish, *Rudolph 83** (US). **Texas:** Arkansas, *Cory 45679* (US); Kenedy Co. 1/2 mi. S of Armstrong, *Lundell & Lundell 14704*** (US); road to Ft. Myers, Beach Fl., *Silveus 6582* (US).

22. Paspalum mosquitiense (Davidse & A. G. Burm.) S. Denham, comb. nov. Basónimo: *Thrasya mosquitiensis* Davidse & A. G. Burm., Ann. Missouri Bot. Gard. 74: 434. 1987. TIPO: Nicaragua. Zelaya: along banks and surrounding gallery forest of Río Likas near Silima Lila, ca. 14°30′N, 83°50′W, 50 m, 5 Mar. 1979, *J. J. Pipoly 4107* (holotipo, MO-3239252 no visto; isotipos, HNMN no visto, SP no visto, US-326034!).

Referencias. Para descripción e ilustración de la especie véase protólogo.

Distribución y ecología. Especie sólo conocida para Honduras y Nicaragua (Fig. 6); crece en bosques o sabanas.

Observaciones. Presenta espiguillas glabras, de 3.4–4 mm de largo y 1.4–1.8 mm de ancho, con la lemma inferior 7-nervia, los racimos son solitarios, con raquis foliáceo y glabro, de 10–16 cm de largo y 2.6–2.8 mm de ancho.

Material estudiado. HONDURAS. **Gracias a Dios:** E de Laguna de Caratasca, *Nelson & Cruz 8621** (MEXU paratipo). NICARAGUA. Sin depart., Comarca del Cabo, Puente Pozo Azul, *Seymour 5803*** (MO paratipo).

23. Paspalum nutans Lam., Tabl. Encycl. 1: 175. 1791. TIPO: América Tropical (sin país), *D. Richard s.n.* (holotipo, P-LA no visto; isotipo, US-2942554!).

Paspalum curvistachyum Raddi, Agrostogr. Bras.: 26. 1823. TIPO: Brasil. Rio de Janeiro: *G. Raddi s.n.* (lectotipo, designado por Chase (J. Washington Acad. Sci. 13: 172. 1923), PI no visto; isotipos, G!, US-2942126!).

Paspalum protensum Trin., Gram. Panic. 108. 1826. *Paspalum heteropodium* Steud., Syn. Pl. Glumac. 1: 19. 1853. TIPO: Mauritius. *F. W. Sieber 29* (holotipo, LE-TRIN no visto; isotipo, US-1445165 no visto).

Paspalum singulare Link, Hort. Berol. 1: 48. 1827. TIPO: Brasil. *F. W. H. A. von Humboldt & A. J. A. Bonpland s.n.* (isotipo, US-80022 no visto).

Paspalum boivinii Steud., Syn. Pl. Glumac. 1: 416. 1854. TIPO: Mauritius. *A. Boivin 1498* (holotipo, P no visto; isotipo, US-2854143!).

Paspalum lloydii Nash, N. Amer. Fl. 17(2): 178. 1912. TIPO: West Indies. Leeward Islands: Dominica, 1903, *F. E. Lloyd 590* (holotipo, NY no visto).

Plantas perennes, rizomas de entrenudos cortos, *cañas* erectas a decumbentes y arraigadas en los nudos basales, la porción erecta de 15–90 cm de alto, 3–4 mm de ancho, laxamente ramificadas, plurinodes; entrenudos de 4–11 cm de largo, ligeramente comprimidos, estriados, glabros; nudos glabros, castaños. *Vainas* de 2–8 cm de largo, aquilladas en la porción superior, glabras a papiloso-pilosas junto a la porción distal, los márgenes pestañosos; *lígulas* membranáceas, de 1–2 mm de largo, castañas; seudolígula ausente u ocasionalmente presente; cuello glabro a piloso; *láminas* lanceoladas, de 4–16 cm de largo, 0.5–1.6 cm de ancho, planas o las basales plegadas, con el nervio medio conspicuo, de base atenuada o redondeada, el ápice agudo, glabras a papiloso-pilosas en ambas caras, los márgenes escabrosos, pestañosos. *Pedúnculos* 1–4 en la última vaina foliar, exertos a subincluidos, hasta de 25 cm de largo, filiformes, glabros a cortamente pubescentes; en ocasiones un pedúnculo presente en la vaina subapical. *Inflorescencias* terminales y axilares; racimos 1–3(4), usualmente 1, solitarios o alternos, arqueados; eje principal nulo o de 1–4 cm de largo; pulvínulos cortamente pilosos; raquis de los racimos de 3.5–6 cm de largo, 0.4–0.6 mm de ancho, triquetro, acanalado a plano, glabro, terminando en una espiguilla desarrollada; pedicelos en pares, iguales a levemente desiguales, el de la espiguilla superior hasta de 1.2 mm de largo, hispídulos; espiguillas dispuestas en 2–4 series irregulares. *Espiguillas* anchamente elipsoides a obovoides, de 1.6–2.1 mm de largo, 1.1–1.4 mm de ancho, plano-convexas, de ápice obtuso a ligeramente agudo, verdosas a pajizas, glabras o cilioladas; *gluma inferior* ausente o raramente presente en la espiguilla inferior o superior del par, cuando presente vestigial o ancha y de ápice obtuso, hasta 1/6 del largo de la espiguilla, centrada, glabra, enervia en la espiguilla superior; ausente a lanceolada, hasta de 1/2 del largo de la espiguilla, excéntrica a centrada, glabra,

enervia a 1-nervia, con el nervio tenue en la espiguilla inferior del par; *gluma superior* 3/4 a 4/5 del largo de la espiguilla, dejando libre el dorso del antecio, membranácea, no papilosa, glabra, en ocasiones ciliolada en el margen, 5-nervia, con un nervio central y los restantes marginales, próximos entre sí; *lemma inferior* tan larga como la espiguilla, membranácea a papirácea, con células alargadas y de paredes marcadas, no papilosa, no sulcada, glabra, los márgenes abruptamente doblados sobre el antecio, 5-nervia, con un nervio central y los restantes próximos al márgen; *pálea inferior* ausente o presente, cuando presente más corta o tan larga como la lemma inferior, ovada, hialina; *flor inferior* presente o ausente, cuando presente con 3 estambres, anteras de 0.5 mm de largo; *antecio superior* anchamente elipsoide, 1.9–2.1 mm de largo, 1.1 mm de ancho, plano-convexo, crustáceo, pajizo, lemma y pálea con células cuadradas, de paredes onduladas, con papilas verrugosas distribuidas regularmente en toda la superficie, centrada en las células, con 2–4 verrugas cada una, micropelos bicelulares escasos hacia el ápice de la pálea; lodículas ca. 0.2 mm de largo; estambres 3, anteras de 0.8 mm de largo. *Cariopsis* subcircular, de 1.1 mm de largo, 0.9–1 mm de ancho; hilo subcircular, 1/4 de la cariopsis; embrión 1/3–1/2 del largo de la cariopsis.

Iconografías. Smith et al., Fl. Il. Catarinense: 1034, fig. 202. 1982; R. W. Pohl, Flora Costaricensis: 432, fig. 160. 1980.

Nombres vulgares. "capim-touceira" (Brasil).

Número cromosómico. $n = 20$ (Davidse & Pohl, 1974).

Distribución y ecología. *Paspalum nutans* habita desde el sur de México, América Central y Caribe, al norte de América del Sur, en Colombia, Venezuela, Guyana, Guayana Francesa y Ecuador; luego en Brasil, sobre la costa Atlantica. Pohl (1980) cita a la especie para Guatemala y Pohl y Davidse (1994) para Isla del Coco (Costa Rica) (Fig. 19). Esta especie ha sido introducida en Mauricio, África (Smith et al., 1982; Pohl & Davidse, 1994). Es frecuente en bosques, selvas, a lo largo de cursos de agua o sobre suelos arenosos, sobre el litoral marino, en lugares soleados; puede hallarse en áreas perturbadas o en bordes de caminos, desde el nivel del mar hasta 2000 m de altura. De acuerdo a Smith et al. (1982) es una especie forrajera apetecida por el ganado, de baja producción.

Observaciones. *Paspalum nutans* se caracteriza por su hábito generalmente decumbente, con cañas plurinodes; los racimos son usualmente solitarios, aunque pueden presentarse 2–3(4) por inflorescencia; las espiguillas, anchamente elipsoides a obovoides, son pequeñas (de 1.6–2.1 mm de largo, 1.1–1.4 mm de ancho), glabras o en ocasiones cilioladas, con la gluma inferior ausente o sólo presente en algunas espiguillas por racimo.

Las afinidades de esta especie con *P. decumbens*, *P. altsonii* y *P. adoperiens* se discuten bajo el tratamiento de cada una de éstas últimas especies.

Material representativo estudiado. ANTILLAS MENORES. Dominica, SE of Portsmouth, *Ernst 2067* (US). BRASIL. **Espírito Santo:** Alegre, *Chase 10046* (US). **Minas Gerais:** Viçosa, *Chase 9448* (MO). **Pará:** Bragança, *Swallen 5017** (US). **Paraná:** Mun. Paranagua, Río Cachoeirinha, *Hatschbach 2256* (US). **Pernambuco:** vic. Pernambuco, Recife, *Chase 7731* (MO, US). **Rio de Janeiro:** Corcovado, vic. of Rio de Janeiro, *Chase 8199* (MO). **Santa Catarina:** Blumenau, *Klein 10374*** (SI, US). **São Paulo:** 10 km S of São Paulo, *Sendulsky 607* (US). COLOMBIA. **Antioquia:** Mun. Urrao, rd. to La Magdalena, 9 km SW of Urrao–Betulia rd., *Brant & Betancur 1629* (MO, SI). **Chocó:** Serranía de Darién along Panama/Colombian Border, *Gentry et al. 16846* (MO). **Guaviare:** río Guayabero, *Cuatrecasas 7521* (US). **Meta:** Villavicencio, *Schiefer 763* (US). **Magdalena:** Santa Marta, *Smith 2156* (BM, G, MO, P, US). COSTA RICA. **San José:** 0.5 km of Barbacoas, *Pohl & Davidse 11407* (MEXU, US). ECUADOR. **Napo:** Jondache, *Asplund 8838* (US). GUAYANA FRANCESA. **Cayena:** 17 Jul. 1921, *Broadway 876* (US). GUYANA. Penal Settlement, W side of río Essequibo, *Hitchcock 17034* (US). HONDURAS. **Francisco Morazán:** Mt. Uyuca, near Zamorano, *McKee 11291* (US). **Intibucá:** La Esperanza, *Medina 32* (SI). MÉXICO. **Chiapas:** Campamento COFOLASA, a 24 km SE de Crucero Corozal, camino a Boca Lacantum., Mpio. Ococingo, *Martinez 7075* (MEXU). NICARAGUA. **Zelaya:** Cayo Palmeta, *Warren Douglas Stevens 20768* (MEXU). PANAMÁ. **Archipiélago de las Perlas:** Isla San José, *Johnston 217* (US). **Coclé:** 4 mi. past Llano Grande on rd. to Cascajal, *Sytsma 3941* (MEXU). **Panamá:** sin loc., 29–30 Oct. 1911, *Pittier 4719* (SI). REPÚBLICA DOMINICANA. Sin prov., S Chiltern Estate betw. Pointe Michel and Soufriere Bay, *Ernst 1117* (US). TRINIDAD Y TOBAGO. St. Anús, *Broadway 5331* (US). VENEZUELA. **Apure:** Distrito Páez, Selva de Cutufí, betw. Cutufí on the Río Cutufí and the Río Sanare, *Davidse & González 21725* (MO). **Aragua:** Par. Nac. Henry Pittier, NW of Maracay, Rancho Grande, *Davidse 3020* (MO, US). **Bolívar:** 30 to 40 km E of Ciudad Piar by winding rd., *Davidse & González 11366* (MO). **Delta Amacuro:** Lower Orinoco, Sacupana, *Rusby & Squires 248* (US). **Falcón:** Maparari, 11 km E de Churuguara, *Wingfield 6485* (MO). **Miranda:** Los Teques, *Chase 12314* (US). **Nueva Esparta:** Isla Margarita, Cerro Copey, *Delascio & González 12268* (MO). **Táchira:** 10 km E of La Fundación, around Represa Dorada, *Liesner & González 10405* (MO).

24. Paspalum oreophilum (A. G. Burm.) S. Denham, comb. nov. Basónimo: *Thrasya oreophila* A. G. Burm., Brittonia 34: 458. 1982. TIPO: Brasil. Minas Gerais: São Gonçalo do Rio das Pedras, roadside descending into valley of Rio

Jequitinhonha, 15 Feb. 1981, *A. G. Burman 591* (holotipo, SP no visto).

Referencias. Para descripción e ilustración de la especie véase protólogo (Burman, 1982: 459).

Distribución y ecología. Endémica de Minas Gerais, crece en los cerrados, alrededor de los 900 m s.m. (Fig. 6).

Observaciones. *Paspalum oreophilum* se distingue por sus 1 a 3 racimos, solitarios a subopuestos, con raquis foliáceo, de 2–2.5 mm de ancho, glabro en la superficie y piloso en los márgenes, con pelos papilosos, dorados hasta de 8 mm de largo, dispuestos en una o dos hileras sobre el márgen. Las espiguillas se disponen sobre el raquis dorso contra dorso o menos frecuentemente con un arreglo tipo "paspaloide"; la gluma superior presenta los nervios prominentes y venillas anastomosadas hacia la porción distal. Esta especie se relaciona con *P. cinerascens* por la presencia de espiguillas con la gluma superior reticulada y la disposición de las espiguilla sobre el raquis que varía de paspaloide a thrasyoide.

Material estudiado. BRASIL. **Minas Gerais:** sin loc., 900 m, *Irwin et al. 27989*/*** (MO).

25. Paspalum orinocense S. Denham, nom. nov. Nombre reemplazado: *Thrasya paspaloides* Kunth, Nov. Gen. Sp 1: 121. 1815 [1816], non *Paspalum paspaloides* (Michx.) Scribn., Mem. Torrey Bot. Club 5: 29. 1894. *Panicum thrasya* Trin., Mem. Acad. Imp. Sci. Saint Petersbourg, Ser. 6, Sci. Math. Seconde Pt. Sci. Nat. 3, 1: 228. 1834. TIPO: Venezuela. May, *F. W. H. A. von Humboldt & A. J. A. Bonpland 16 1/2* (lectotipo, designado por Burman (Bot. J. Linn. Soc. 82: 339. 1981), B-W-1618 no visto; isotipo, US no visto).

Referencias. Para descripción de la especie véase Burman (1985 [1987]); ilustración en Luces (1942: 84).

Número cromosómico. $n = 20$ (Davidse & Pohl, 1972b).

Distribución y ecología. Esta especie ha sido escasamente coleccionada en un área restringida de Venezuela, a orillas del río Orinoco, en la región de Great Rapids, hasta los 100 m de elevación (Fig. 8). Filgueiras (1991) cita a la especie para Brasil, en el Distrito Federal, aunque probablemente se trate de un ejemplar erróneamente determinado de *P. thrasyoides* o *P. trinitense*, especies afines por la pilosidad de la lemma inferior, pero de más amplia distribución.

Observaciones. Especie similar a *P. setosum* por presentar espiguillas con un callo en la base, con el antecio más corto que la gluma superior y la lemma inferior, por la ausencia de la gluma inferior y por las cañas profusamente ramificadas; *P. orinocense* se separa por la pilosidad densa de la gluma superior (vs. escasamente pilosa o glabra en *P. setosum*), por sus cañas erectas (vs. decumbentes a postradas en *P. setosum*) y por el margen del raquis piloso (vs. glabro en *P. setosum*). Ambas especies presentan una distribución geográfica restringida y similar.

El epíteto específico del nombre nuevo hace referencia a su distribución a orillas del Orinoco medio.

Material estudiado. VENEZUELA. **Amazonas:** Río Carinagua, 8 km S of Puerto Ayacucho, *Davidse 2743*** (US, VEN). **Bolívar:** Cedeño, on rd. to Puerto Ayacucho, *Holst & Werff 2599* (US); Cedeño, *Guanchez & Huber 4844* (SI); bordes del Orinoco, *Chaffanjon 280** (US).

26. Paspalum parvulum (A. G. Burm.) S. Denham, comb. nov. Basónimo: *Thrasya parvula* A. G. Burm., Brittonia 32: 217. 1980. TIPO: Brasil. Pará: Jaramacarú, Lagedo próx. barranco, 27 May 1957, *W. A. Egler 310* (holotipo, MG-22170 no visto).

Referencias. Para descripción e ilustración véanse protólogo y Burman (1985 [1987]).

Distribución y ecología. Especie sólo conocida por la colección tipo, procedente de Pará, Brasil (Fig. 6).

Observaciones. *Paspalum parvulum* se distingue por presentar ambas glumas reducidas (1/6–1/3 de la espiguilla) y la lemma inferior membranácea; las plantas alcanzan los 55 cm de alto, los racimos miden 2–4.5 cm de largo y los pedicelos son largamente ciliados. La pálea y flor inferior son ausentes. *Paspalum parvulum* se relaciona con *P. achlysophilum* y *P. scandens* por la consistencia membranácea o hialina de la lemma inferior. La posición "thrasyoide" de las espiguillas sobre el raquis y la lemma sulcada relacionan a esta especie con las restantes especies del subgénero *Harpostachys*.

27. Paspalum peckii F. T. Hubb., Proc. Amer. Acad. Arts 49: 495. 1913. TIPO: Belize. Manatee Lagoon, 18 July 1905, *M. E. Peck 71* (holotipo, GH no visto; isotipo, US-2942524!).

Plantas perennes, cespitosas; *cañas* erectas, de 75–82 cm de alto, simples; entrenudos glabros; nudos pilosos. *Vainas* carinadas, ciliadas en los márgenes; *lígulas* membranáceas, de 2–3 mm de largo; seudolígula pilosa; cuello piloso; *láminas* linear-lan-

ceoladas, de 14–30 cm de largo, 0.5–0.8 cm de ancho, planas, de base angostada, esparcidamente pilosas en la superficie a glabras, los márgenes escabriúsculos, el ápice agudo. *Pedúnculos* 1–2 en la última vaina foliar. *Inflorescencias* terminales y axilares; racimos 2–3, subopuestos, levemente falcados; raquis de los racimos de 6–13 cm de largo, 1.9 mm de ancho, plano, con cortas extensiones laterales, escabroso, esparcidamente ciliado, terminando en una espiguilla desarrollada; pedicelos en pares, desiguales, el de la espiguilla superior hasta de 1 mm de largo, glabros, escabrosos; espiguillas dispuestas en 4 series. *Espiguillas* elipsoides, de 2.5–2.7 mm de largo, 1.2–1.3 mm de ancho, plano-convexas a levemente cóncavo-convexas, pajizas, glabras; *gluma inferior* dimorfa: ausente o presente en la espiguilla superior del par, cuando presente, ancha y de ápice obtuso, hasta 1/6 del largo de la espiguilla, centrada, glabra, enervia; rudimentaria, de base ancha y ápice recto o hasta 1/2 de la espiguilla y aguda, centrada a levemente excéntrica, glabra o ciliolada en los márgenes, enervia o 1-nervia, en la espiguilla inferior del par; *gluma superior* levemente más corta que la espiguilla, no papilosa, glabra, 5–7-nervia, con un nervio central y los restantes marginales, próximos entre sí; *lemma inferior* tan larga como la espiguilla, cartácea, no papilosa, levemente sulcada a plana, glabra, 5–7-nervia, con un nervio central y los restantes marginales, próximos entre sí, con los márgenes doblados sobre el antecio; *pálea inferior* tan larga como la lemma, hialina, con los nervios endurecidos; *flor inferior* ausente o estaminada, estambres 3, anteras de 1 mm de largo; *antecio superior* elipsoide, levemente más corto que la espiguilla, de 2.2 mm de largo, 1–1.1 mm de ancho, plano-convexo, crustáceo, pajizo, lemma y pálea con celulas cuadradas, de bordes ondulados, con papilas verrugosas regularmente distribuidas, centradas en las células, con 4–5 verrugas cada una, micropelos bicelulares hacia el ápice de la lemma y de la pálea, con la célula apical 2 veces más larga que la basal; lodículas 0.3 mm de largo; estambres no vistos. *Cariopsis* no vista.

Iconografía. A. Chase, Contr. U.S. Natl. Herb. 28: 97, fig. 51. 1929.

Distribución y ecología. Especie endémica de Bélice, en Mesoamérica (Fig. 19).

Observaciones. Sólo se observó un fragmento del material tipo, y no hay registros de nuevas colecciones. En la descripción original de la especie, el autor la relaciona con *Paspalum pilosum*, distinguiendo a ambas por el número de racimos (usualmente uno en *P. pilosum*), el tamaño y pilosidad de las láminas (más cortas y menos pubescentes en *P. peckii*) y la textura de la lemma inferior (más delgada en *P. peckii*). En el presente tratamiento se considera a *P. peckii* como especie válida hasta tanto se obtenga más material de estudio. La observación del material tipo de esta especie permite separarla de *Paspalum pilosum* por el número de racimos (2 a 3 vs. 1), ancho del raquis (1.9 mm vs. 0.8–1.5 mm) y por la forma y tamaño de las espiguillas (elipsoides, de 2.5–2.7 por 1.2–1.3 mm vs. anchamente elipsoides, de (2.2–)2.4–3 por 1.5–1.8 mm).

28. Paspalum petilum Chase, J. Washington Acad. Sci. 27(4): 145. 1937. TIPO: British Guiana. Essequibo: Konawaruk River, China Creek, Sep. 1906, *A. W. Bartlett 8569* (holotipo, US-1298462!, foto SI!; isotipo, K no visto, foto SI!).

Paspalum dispar var. *marahuacense* H. Rodr., Ernstia 52: 1. 1989. TIPO: Venezuela. Terr. Fed. Amazonas: Dpto. Atabapo, 17 Oct. 1988, *H. Rodríguez 2816* (holotipo, MY no visto; isotipos, K!, MO-4045892!, SI!, VEN-255550 no visto).

Plantas perennes, cespitosas; *cañas* erectas y decumbentes a estoloníferas, porción erecta de 15–40 cm de alto, 1–1.2 mm de diámetro, laxamente ramificadas, plurinodes; entrenudos de 2–5 cm de largo, comprimidos, estriados, glabros; nudos barbados, con cortos pelos blanquecinos. *Vainas* mayores que los entrenudos, superpuestas, glabras, con los márgenes densamente pestañosos; *lígulas* membranáceas, de 1–2 mm de largo, castañas; seudolígula ausente; cuello glabro a cortamente piloso; *láminas* lineares a linear-lanceoladas, 4–15 cm de largo, 0.3–0.4 cm de ancho, ascendentes, planas, de base atenuada y ápice agudo, el nervio medio levemente aquillado, glabras, los márgenes lisos. *Pedúnculos* 1–4, emergiendo de la última vaina foliar, levemente exertos, hasta de 10 cm de largo, filiformes, glabros. *Inflorescencias* terminales y axilares; racimos 1, raro 2, recto a ligeramente arqueado, que no sobrepasan la altura de las láminas; eje principal nulo o hasta de 1 cm de largo; pulvínulos cortamente pilosos; raquis de los racimos de 1–3(–4) cm de largo, 0.4 mm de ancho, triquetro, acanalado, hispídulo en la cara abaxial a glabro, margen glabro a esparcidamente ciliado, terminando en una espiguilla desarrollada; pedicelos en pares, desiguales, el de la espiguilla superior ca. 0.7 mm de largo, escabriúsculos; espiguillas no imbricadas, irregularmente distribuidas en 2–4 series. *Espiguillas* elipsoides a obovoides, de 1.4–2 mm de largo, 1–1.2 mm de ancho, plano-convexas, de ápice agudo, delicadamente pubescentes, con pelos hasta de 0.5 mm de largo sobre

las glumas y lemma inferior; *gluma inferior* dimorfa: de base ancha y ápice agudo, 1/4 del largo de la espiguilla, centrada, densamente pilosa en los márgenes, con pelos brillosos, enervia, en la espiguilla superior del par; triangular a lanceolada o acuminada, 1/2–3/4 del largo de la espiguilla, excéntrica, densamente pilosa en los márgenes, con pelos brillosos, enervia a 1-nervia, en la espiguilla inferior; *gluma superior* 1/2 a 2/3 del largo de la espiguilla, densamente pubescente hacia los márgenes, con pelos adpresos, esparcidamente pilosa en el resto de la superficie, no papilosa, 3-nervia; *lemma inferior* tan larga como la espiguilla, membranácea a papirácea, con pilosidad similar a la presente en la gluma superior, con las paredes celulares marcadas, no papilosa, no sulcada, 3–5-nervia, cuando 5-nervia, un nervio central y los marginales próximos entre sí, con los márgenes doblados sobre el antecio; *pálea inferior* presente o ausente, cuando presente lanceolada, 3/4 del largo de la espiguilla, hialina; *flor inferior* ausente; *antecio superior* anchamente elipsoide a obovoide, 1.3–1.6 mm de largo, 1.1 mm de ancho, planoconvexo, crustáceo, pajizo, lemma y pálea con células cuadradas a rectangulares, de paredes onduladas, lisas o las células apicales con papilas simples; lodículas ca. 0.2 mm de largo; estambres 3, anteras ca. 0.9 mm de largo. *Cariopsis* elipsoide, ca. 1 mm de largo, 0.5 mm de ancho; hilo anchamente elíptico, 1/4 de la cariopsis; embrion 1/3 del largo de la cariopsis.

Iconografía. E. Judziewicz, Fl. Guianas: 503, fig. 86 a–d. 1990.

Distribución y ecología. Paspalum petilum se distribuye en Guyana, sur de Venezuela y norte de Brasil (Fig. 11). Habita en márgenes de ríos o arroyos, bordeando los bosques tropicales, sobre suelos rocosos o arenosos, entre 100–1800 m s.m.

Observaciones. Esta especie se caracteriza por sus cañas decumbentes a estoloníferas, inflorescencias terminales formadas usualmente por un racimo de 1–3(–4) cm de largo, que no sobrepasan la altura de las láminas, espiguillas pequeñas (1.4–2 mm de largo), gluma superior 1/2–3/4 del largo de la espiguilla y glumas y lemma inferior densamente pilosas en los márgenes y esparcidamente pilosas en la superficie.

Esta especie es similar a *P. decumbens* en su hábito, tamaño y forma de las espiguillas, pero se distingue por la pilosidad de las espiguillas (delicadamente pubescentes en *P. petilum* y glabras en *P. decumbens*).

Material representativo estudiado. BRASIL. **Amazonas:** Río Tucano, *Maguire et al. 60323* (US). BRITISH GUIANA. Reg. Cuyumi-mazaruni, Pakaraima Mtn. Karowrieng R, 0.5–1 km SE Maipuri Falls, *Hoffman et al. 3057* (MO, US). VENEZUELA. **Amazonas:** Dpto. Atabapo, Cerro Marahuaca, *Liesner 24975* (MO, US). **Bolívar:** Gran Sabana, ca. 10 km SW of Karaurin Tepui, *Liesner 23790** (US).

29. Paspalum pilosum Lam., Tabl. Encycl. 1: 175. 1791. *Dimorphostachys pilosa* (Lam.) E. Fourn., Mexic. Pl. 2: 14. 1886. TIPO: Sin país. América Tropical, *L. C. M. Richard s.n.* (holotipo, P-LA no visto; isotipo, US-2942529!).

Panicum monostachyum Kunth, in Humboldt, Bonpland & Kunth, Nov. Gen. Sp. 1: 96. 1816. *Dimorphostachys monostachya* (Kunth) E. Fourn. ex Hemsl., Biol. Centr.-Amer., Bot. 3: 499. 1882–1886, non *Dimorphostachys monostachya* (Kunth) E. Fourn., Mexic. Pl. 2: 14. 1886. TIPO: Venezuela. Amazonas: San Fernando de Atabapo, *F. W. H. A. von Humboldt & A. J. A. Bonpland s.n.* (lectotipo, designado por Chase (Contr. U.S. Natl. Herb 28(1): 97. 1929), P!, foto SI!; isotipo, US-81114!).

Thrasya villosa Hitchc., Proc. Biol. Soc. Washington 40: 84. 1927. *Paspalum peregrinum* A. G. Burm. & Filg., Acta Bot. Venez. 14(4): 91. 1985 [1987]. TIPO: Panamá. Eastern Chiriquí: savannas at Cerro Vaca, 900–1136 m, 25–28 Dec. 1911, *H. F. Pittier 5363* (holotipo, US-715585 no visto).

Thrasya venezuelana Chase, J. Washington Acad. Sci. 42(4): 122. 1952. *Paspalum venezuelanum* (Chase) A. G. Burm., Acta Bot. Venez. 14(4): 90. 1985 [1987], comb. illeg. TIPO: Venezuela. Distrito Federal: sabanas de Cotiza, 11 Mar. 1940, *A. Chase 12407* (holotipo, US-1762130!, foto SI!; isotipo, VEN no visto).

Plantas perennes, rizomas de entrenudos cortos; *cañas* erectas a decumbentes o arraigadas en los nudos basales, de 40–100 cm de alto, 0.2–0.3 cm de diámetro, simples o ramificadas en los nudos medios, con ramas divergentes; entrenudos de 5–12 cm de largo, ligeramente comprimidos, pajizos, glabros; nudos glabros a densamente pilosos, castaños. *Vainas* de 5–25 cm de largo, aquilladas, glabras a papiloso-pilosas en la porción superior, los márgenes pestañosos; *lígulas* membranáceas, de 1–2 mm de largo, castañas; seudolígula formada por un mechón de pelos; cuello densamente piloso; *láminas* linear-lanceoladas, de 10–40 cm de largo, 0.4–1(–1.4) cm de ancho, planas o plegadas, de base redondeada o angostada y ápice acuminado, el nervio medio manifiesto, pubescentes a papiloso-pilosas, los márgenes pestañosos. *Pedúnculos* 1–4 en la última vaina foliar, exertos a parcialmente incluidos, hasta de 35 cm de largo, glabros a cortamente pilosos, frecuentes también en los nudos medios. *Inflorescencias* terminales y axilares; racimos 1–2, solitarios o alternos, solitarios en las inflorescencias de los nudos medios, arqueados; eje principal nulo o hasta de 5 cm de largo, comprimi-

do, glabro; pulvínulos pilosos; raquis de los racimos de 4–15(–20) cm de largo, 0.8–1.5 mm de ancho, triquetro o con cortas extensiones laterales, la cara adaxial glabra, la abaxial hispídula, los márgenes glabros a esparcidamente ciliados, terminando en una espiguilla desarrollada; pedicelos en pares, el de la espiguilla superior hasta de 0.5 mm de largo, hispídulos, con el ápice ensanchado; espiguillas en pares, irregularmente dispuestas en 2–4 series. *Espiguillas* anchamente elipsoides, de (2.2–)2.4–3 mm de largo, 1.5–1.8 mm de ancho, cóncavo-convexas, pajizas a verdosas o con tíntes violáceos, glabras; *gluma inferior* dimorfa: ausente o ancha y de ápice obtuso, hasta 1/6 de la espiguilla, centrada, glabra, enervia, en la espiguilla superior del par; ancha y obtusa o lanceolada a acuminada, 1/6–3/4 del largo de la espiguilla, excéntrica, glabra, 1–3-nervia, el nervio central liso o escabroso, en la espiguilla inferior; en ocasiones más o menos isomorfas; *gluma superior* ligeramente menor que la espiguilla, dejando libre el ápice del antecio, o subiguales, papirácea, finamente papilosa, 5-nervia, con el nervio medio en ocasiones mucronado, los restantes de equidistantes a marginales, usualmente verdosos; *lemma inferior* tan larga como la espiguilla, papilosa, sulcada, 5-nervia, con un nervio central y los marginales próximos entre sí, frecuentemente endurecidos, con los márgenes doblados sobre el antecio; *pálea inferior* tan larga como la espiguilla a veces más corta, hialina, glabra o con los márgenes apicales ciliados; *flor inferior* presente o ausente, cuando presente estambres 3, anteras de 0.9–1.1 mm de largo; *antecio superior* anchamente elipsoide, 2.2–2.7 mm de largo, 1.2–1.5 mm de ancho, plano-convexo, crustáceo, pajizo, lemma y pálea con celulas cuadradas, de paredes onduladas, con papilas verrugosas distribuidas regularmente, centradas, con 5–6 verrugas cada célula, ocasionalmente con escasos micropelos bicelulares hacia el ápice de la pálea; lodículas ca. 0.4 mm de largo; estambres 3, anteras de 0.9–1.1 mm de largo. *Cariopsis* anchamente elipsoide, 1.2–1.4 mm de largo; hilo elíptico, 1/3 de la cariopsis; embrión 1/2 de la cariopsis.

Iconografía. E. Judziewicz, Fl. Guianas: 503, fig. 86 E. 1990.

Nombres vulgares. "capin felpudo" (*Valls 1218, 1219*, Brasil), "zacate camalote" (Beetle et al. 1999, México).

Número cromosómico. $n = 40$ en ejemplares de Costa Rica y Venezuela (Pohl & Davidse, 1971; Davidse & Pohl, 1974; Pohl, 1980).

Distribución y ecología. Habita en México y América Central, Colombia, Venezuela y Guayana Francesa, hasta Bolivia, Perú y Brasil (Fig. 10). Es frecuente en el cerrado, en campos abiertos, campos rupestres, o bordes de bosques, a lo largo de cursos de agua o sobre suelos rocosos, arenosos y calizos, también crece en bordes de caminos, plantaciones de café y áreas perturbadas; entre 0–1900 metros de altura.

Observaciones. *Paspalum pilosum* se caracteriza por presentar espiguillas glabras, con la gluma inferior dimorfa; la gluma superior levemente más corta que la espiguilla o subigual, 5-nervia, lemma inferior 5-nervia, papilosa y con el dorso longitudinalmente sulcado; láminas pubescentes a papiloso-pilosas, de márgenes pestañosos y racimos 1–2, hasta de 15(–20) cm de largo.

Si bien el desarrollo de la gluma inferior es variable, ésta se encuentra comúnmente reducida en la espiguilla superior del par y más desarrollada en la espiguilla inferior, alcanzando hasta 3/4 del largo de la espiguilla. También puede observarse la gluma inferior reducida en ambas espiguillas (en los ejemplares *Buchtien 14, Killip & Smith 22528, Hitchcock 19909, 8130, Roe et al. 1787, Pohl & Calderón 10050* y *Rúgolo & Villavicencio 1936*).

Los ejemplares *Davidse et al. 17479* y *Berry 506* presentan la gluma superior papilosa. Por otra parte, el ejemplar *Irwin et al. 19003* presenta espiguillas con pelos delicados sobre la gluma superior.

El raquis de los racimos usualmente posee los márgenes glabros o esparcidamente ciliados; sin embargo se ha observado ejemplares con los márgenes esparcida a densamente piloso-pestañosos, con pelos papilosos, blanquecinos hasta 4 mm de largo, como por ejemplo *Huber & Alarcón 7831, Soderstrom & Carvalho 1158, Harley et al. 17387, Anderson et al. 36112, Irwin et al. 9650, Zuloaga et al. 4593* y *Hitchcock 8130.*

El ejemplar *Irwin et al. 9650* posee racimos hasta de 20 cm de largo y en el espécimen *Noblick 3063* pueden observarse tres racimos. *Irwin et al. 13764* está, aparentemente, afectado por carbones.

Existen dos ejemplares de *Pohl & Calderón 10050* (MEXU), de Costa Rica; uno de ellos corresponde a *P. pilosum* y el segundo a *P. nutans.*

Paspalum pilosum y *P. nutans* se diferencian porque en la última especie la gluma inferior es generalmente ausente o sólo presente en algunas espiguillas del racimo, las espiguillas son anchamente elipsoides a obovadas, la gluma superior y lemma inferior son membranáceas a papiráceas, no papilosas y las láminas son lanceoladas.

Paspalum unispicatum se diferencia de *P. pilosum* principalmente por presentar rizomas alarga-

dos y por las espigillas de 2.8–3.6(–3.9) mm de largo y 1.6–1.8 mm de ancho.

Paspalum peregrinum y *Thrasya venezuelana* presentan vainas y láminas densamente pilosas, racimos ocasionalmente ramificados en su base, espiguillas pilosas y gineceo piloso. Denham y Aliscioni (2003) estudiaron nuevas colecciones de *P. peregrinum* que presentan, en la misma planta, macollos con la morfología descripta para esa especie y macollos cuya morfología corresponde a *P. pilosum*. Por medio de la detección de quitina en las plantas analizadas, las autoras pudieron comprobar que ambas entidades, *P. peregrinum* y *T. venezuelana*, constituyen ejemplares anómalos de *P. pilosum*, con modificaciones morfológicas causadas por una infección fúngica. Consecuentemente, Denham y Aliscioni (2003) transfieren ambos taxones bajo la sinonimia de *P. pilosum*. Especímenes de *P. pilosum* con vainas, láminas y espiguillas densamente pilosos y gineceos anormales también fueron reportados por Chase (ined.), quien menciona una posible infección fúngica en estas plantas.

Al realizar la combinación *Paspalum venezuelanum* (Chase) A. G. Burm., Burman (1985 [1987]) cita erróneamente el basónimo *Thrasya venezuelana* Chase, y por lo tanto, de acuerdo al artículo 33.3 del Código Internacional de Nomenclatura Botánica (Greuter et al., 2000), esta combinación no es válida.

Material representativo estudiado. BELIZE. **Stann Creek:** Possum Point Biological Station, *Vincent et al. 6184* (MO). BOLIVIA. **La Paz:** San Carlos, *Buchtien 14* (US). **Prov. Nor-Yungas:** camino Yolosa–Caranavi, desvío a Coroico, a 9 km de Yolosa, *Rúgolo & Villavicencio 1936* (SI). **Santa Cruz:** Velasco, Parque Nacional Noel Kempff M., Catarata Ahlfeld, *Killeen et al. 5451* (MEXU, MO, SI). BRASIL. **Amazonas:** in vicinibus Barra, Prov. Río Negro, *Spruce 22* (G, US). **Bahía:** 24 km SW of Belmonte, on road to Itapebi, *Harley et al. 17387* (K, MO); Rio Lencois a cima do Serrano Lencois, *Noblick 3063* (CTES). **Distrito Federal:** ca. 20 km NE of Brasília, *Irwin et al. 9650* (MO). **Goiás:** Serra dos Pirineus, 75 km N of Corumbá de Goiás on road to Niquelandia, *Irwin et al. 19003* (MO, US); Serra dos Cristais, ca. 15 km E of Cristalina, *Irwin et al. 13764* (US). **Mato Grosso:** ruta de Chapada dos Guimarães a Nova Brasilandia, 1 km E de Chapada dos Guimarães, *Rua et al. 247* (CTES). **Minas Gerais:** Serra do Cipó, *Anderson et al. 36112* (MO, US); Rodovía de Cardeal Mota a Conceição do Mato Dentro, BR-010, 22–24 km de Cardeal Mota, *Zuloaga et al. 4593* (MO, SI). **Pará:** Belém, *Soderstrom & Carvalho 1158* (MO). **Paraná:** Jaguariaiva, *Dusén 14925* (BM, MO, SI). **Rio de Janeiro:** Macieiras, Serra de Itatiaia, *Chase 8346* (US). **Rondônia:** Porto Velho, *Valls 1218* (CTES). **São Paulo:** Itararé, *Dusén 13507* (SI). COLOMBIA. **Antioquia:** Guatapé, *Pohl 15445* (MO). **Cauca:** carretera Calipopayan, entre Mondomo y Pescador, *Zuloaga & Londoño 4190** (MO, SI); Buenaventura, *Hitchcock 19909* (US). **Chocó:** Hoya del Río San Juan, Andagoya, *Forero et al. 5117* (MO). **Cundinamarca:** 4 km SW of Fusagusuga, *Davidse et al. 5556* (MO). **Valle del Cauca:** around Calí, W side of Cauca valley, *Pittier 659* (US). **Santander:** Mesa de Los Santos, *Killip & Smith 15112* (US). COSTA RICA. **Guanacaste:** Par. Nac. Rincón de La Vieja, *Davidse et al. 23441* (MO). **Puntarenas:** Buenos Aires, *Pohl & Calderón 10075* (MO). **San José:** 1 km S of Rivas, 6 km NE of San Isidro del General, *Pohl & Calderón 10050* (MEXU). EL SALVADOR. **Chalatenango:** along Hwy. 4, 4 km SSE of La Palma, *Pohl & Davidse 11896* (MO). GUATEMALA. **Guatemala:** 3 km S of Quezaltepeque on CA-10, Chiquimula, *Harmon & Dwyer 3690* (MO). GUAYANA FRANCESA. **Cayena:** 1835, *Leprieur s.n.* (G, P). HONDURAS. **Comayagua:** along new Hwy., 10 km NW of Siguatepeque, *Pohl 12762* (MO). **Cortés:** Lago de Yojoa, 60 km SE de San Pedro Sula, *Izaguirre 148* (MO). **El Paraíso:** along Hwy. 4, 25 km E of El Zamorano, *Pohl & Davidse 11921* (MO). **Francisco Morazán:** sin loc., *Rodriguez 1561* (MEXU). **Olancho:** 6 km SW of Dulce Nombre de Culmí, along Hwy. 3, *Pohl & Davidse 12443* (MO). MÉXICO. **Chiapas:** 3–5 km above Jaltenango along rd. to Finca Prusia, *Breedlove 38572* (MEXU). **México:** 5 km S of Temascaltepec, *Roe et al. 1787* (MEXU). **Michoacán:** along rd. from Tsitzio-Tiquicheo-huetamo, *Sohns 893* (US). **Oaxaca:** San Pedro Pochutla, 4 km de Piedra de Lumbre, *Gonzalez-Ledesma & Catalán-Hev 598* (MEXU). **Tabasco:** Huimanguillo, *Cowan et al. 3249* (MEXU). NICARAGUA. **Zelaya:** betw. Waspan and Ulwas, *Pohl & Davidse 12287* (MO). PANAMÁ. **Chiriquí:** foothills, vic. El Boquete, *Hitchcock 8192* (SI). **Panamá:** Chorrera, *Hitchcock 8130* (SI). **Veraguas:** along rd. to radio tower on Cerro San Cristobal, near Pan. Am. Hwy., 9 Km W of bridge over Río Cobre, *Nee 10163* (MO). PERÚ. **Ayacucho:** Aina betw. Huanta and Río Apurimac, *Killip & Smith 22528* (US). TRINIDAD Y TOBAGO. Port of Spain, *Hitchcock 9987* (US). VENEZUELA. **Amazonas:** entre la pista y Santa Bárbara del Orinoco, *Berry 506* (MO); Atabapo, Santa Bárbara de Orinoco, 3 km W of junction río Orinoco and Río Ventuari, *Davidse et al. 17479* (MO). **Anzoátegui:** Distr. Freites, Burro trail betw. San Durrial and Los Pajaritos, *Davidse & González 19794*** (MO, SI). **Apure:** near Capuana, E bank of the Río Orinoco, *Davidse et al. 16795* (MO). **Bolívar:** Distr. Roscio, Hato La Divina Pastora, aprox. 8 km N de Santa Elena de Uairén, *Huber & Alarcón 7831* (MO). **Distrito Federal:** Par. Nac. El Avila, *Trejos 45102* (MO). **Guárico:** Estación Biológica Los Llanos, 10 km SSE of Calabozo, *Davidse 2917* (MO). **Mérida:** Fac. Cs. Forestales, alrededores de la Facultad, *Morrone et al. 4721* (SI). **Monagas:** via cueva del Guacharo, *Montes 1661* (MO).

30. **Paspalum procerum** S. Denham, nom. nov. Nombre reemplazado: *Thrasya hitchcockii* Chase, J. Washington Acad. Sci. 17: 142. 1927, non *Paspalum hitchcockii* Chase, Contr. U.S. Natl. Herb. 28: 160. 1929. TIPO: Panamá. Prov. Panamá: Chorrera, at the edge of a copse, on a hill, 16 Sep. 1911, *A. S. Hitchcock 8140* (holotipo, US!; isotipo, K no visto).

Referencias. Para descripción de la especie e ilustración de las espiguillas véase Burman (1985 [1987]).

Distribución y ecología. Esta especie se distribuye en Costa Rica (Davidse, 1994; Burman, 1985

[1987]), Panamá y Venezuela (Fig. 6); crece en sabanas o bordes de bosques, entre 700–1400 m s.m.

Observaciones. *Paspalum procerum* presenta espiguillas con un arreglo tipo "paspaloide" sobre el raquis, las plantas son de gran porte, de 100 cm de altura, con cañas decumbentes y ramificadas, láminas foliares hasta de 30 cm de largo y racimos usualmente solitarios, de 7–18 cm de largo y 1.5–2 mm de ancho; las espiguillas miden de 3.2–3.5 mm de largo y 1.7–1.9 mm de ancho.

El epíteto específico del nombre nuevo hace referencia al tamaño de las plantas de la especie.

Material estudiado. PANAMÁ. **Chiriquí:** 26 km N of David, rd. to Boquete, *Davidse & D'Arcy 19136* (MEXU). **Panamá:** Tecumén, *Dwyer 2563A*** (MO). VENEZUELA. **Distrito Federal:** sabanas de Cotiza, *Chase 12403* (US); Caracas, *Woronow 7408* (US), *Pittier 9517** (US). **Miranda:** San Jose de las Morros, *Davidse & Tillett 4515* (US).

31. Paspalum scandens Tutin, J. Bot. 72(864): 338. 1934. *Thrasya scandens* (Tutin) Soderstr. & A. G. Burm., Brittonia 32: 220. 1980. TIPO: British Guiana. Kaieteur savanna, Potaro River, ca. 1100 ft., 28 Aug 1933, *T. G. Tutin 631* (holotipo, BM no visto; isotipos, K!, US!).

Thrasya guianensis Swallen, Mem. New York Bot. Gard. 9: 250. 1957. TIPO: British Guiana. Sagaraimadai, upper Mazaruni River, 550 m, 16 Nov. 1951, *B. Maguire & D. B. Fanshawe 32621A* (holotipo, US!; isotipo, K!).

Referencias. Para descripción de la especie e ilustración de las espiguillas véase Burman (1985 [1987]).

Distribución y ecología. Endémica de las Guayanas, es frecuente en áreas perturbadas, entre 400–1400 m s.m. (Fig. 6).

Observaciones. Esta especie, al igual que *P. achlysophillum* y *P. parvulum*, presenta la lemma inferior membranácea; sin embargo, se diferencia por sus plantas de mayor porte, con cañas de 70–100 cm de alto (vs. hasta de 55 cm), sus racimos más largos (4–11 cm vs. 2–4.5 cm) y la gluma superior 3–5-nervia (vs. 7-nervia o enervia). Sus láminas son lanceoladas y sus inflorescencias presentan 1–2 racimos, solitarios a subopuestos.

Material estudiado. GUAYANA FRANCESA. **Cayena:** Oyapocha, *Hoock 804* (US). **St. Laurent du Maroni:** Roche Koutou, *Granville et al. 9333* (MO). BRITISH GUIANA. Kaieteur Plateau, *Maguire & Fanshawe 23456*/**** (MO, US), *Cowan & Soderstrom 1821* (US); Potaro-siparuni, *Hahn et al. 4516* (US).

32. Paspalum schumannii (Pilg.) S. Denham, comb. nov. Basónimo: *Panicum schumannii* Pilg., Bot. Jahrb. Syst. 30(1): 134. 1901. *Thrasya schumannii* (Pilg.) Pilg., Pflanzenr. ed. 2, 14e: 69. 1940. TIPO: Brasil. Matto Grosso: "haufig zerstreut auf Bachwiesen in Quellgebiet des Batoví," Jun. 1899, *H. Meyer 683* (holotipo, B no visto; isotipo, US-80976 no visto).

Referencias. Para descripción de la especie e ilustración de las espiguillas véase Burman (1985 [1987]).

Distribución y ecología. Especie conocida sólo por el material tipo, que crece en el área de Batoví, en Mato Grosso, Brasil (Fig. 15).

Observaciones. Es característico de esta especie la gluma superior hasta 1/3 del largo de la espiguilla y enervia, el raquis de los racimos con pelos papilosos, rígidos y dorados dispuestos en el márgen. *Paspalum auricomum* también presenta el raquis de los racimos piloso, pero se diferencia de *P. schumannii* por presentar pelos tanto en la superficie como en los márgenes del raquis y por las espiguillas pilosas.

33. Paspalum seminudum (A. G. Burm.) S. Denham, comb. nov. Basónimo: *Thrasya seminuda* A. G. Burm., Brittonia 32: 218. 1980. TIPO: Brasil. Mato Grosso: Catagui-iamain (Campo dos Urupás), Dec. 1918, *Rondón 1765* (holotipo, RB-89828 no visto).

Referencias. Para descripción e ilustración de la especie véanse protólogo y Burman (1985 [1987]).

Distribución y ecología. Crece en la zona de Serra dos Parecís, en Mato Grosso, Brasil, preferentemente sobre rocas (Burman, 1980; Fig. 6).

Observaciones. Existen escasas colecciones de *P. seminudum.* Sus inflorescencias presentan 1–3 racimos, de 14–30 cm de largo; sus espiguillas, 3.5–4 mm de largo, presentan la lemma inferior más larga que la gluma superior y el antecio superior. Se destacan las lígulas de 5–6 mm de largo. Burman (1980) relaciona a esta especie con *Thrasya petrosa* [= *P. foliiforme*].

34. Paspalum setosum (Swallen) S. Denham, comb. nov. Basónimo: *Thrasya setosa* Swallen, Fieldiana Bot. 28(1): 17. 1951. TIPO: Venezuela. Amazonas: vic. of Sanariapo, near Río Sanariapo, tributary of Orinoco river, 100 m, 8 Sep. 1944, *J. A. Steyermark 58502* (holotipo, US-1911654!; isotipo, F no visto).

Referencias. Para descripción de la especie e ilustración de las espiguillas véase Burman (1985 [1987]).

Distribución y ecología. *Paspalum setosum* crece en Venezuela, con una distribución restringida a la zona entre Puerto Ayacucho y Sanariapo, en el estado de Amazonas y en el sur del estado de Bolivar (Fig. 8); crece sobre las rocas, desde el nivel del mar a 200 m de elevación.

Observaciones. Véanse comentarios bajo *Paspalum orinocense.*

Material estudiado. VENEZUELA. **Amazonas:** Puerto Ayacucho, *Huber 1281* (MO); Atures, Puerto Ayacucho, *Huber 4752*/*** (MO, VEN), *Groger 528* (MO). **Bolívar:** Piedra Marimare, *Wurdack & Monacino 39984* (US).

35. Paspalum subfalcatum (Döll) Tutin, J. Bot. 72: 338. 1934. *Panicum subfalcatum* Döll, Fl. Bras. 2(2): 181. 1877. TIPO: Brasil. Amazonas: "prope Paruné et Rio Vaupés," Nov. 1852, *R. Spruce 2820* (holotipo, no localizado; isotipos, K no visto, P!, foto SI!, US-81115!). Figura 22.

Plantas perennes, con rizomas de entrenudos cortos; *cañas* erectas a decumbentes, de 15–45 cm de alto, 0.6–2 mm de ancho, simples a ramificadas; entrenudos de 7–15 cm de largo, comprimidos, glabros; nudos glabros o pilosos, con pelos blanquecinos, castaños, angulosos. *Vainas* más cortas que los entrenudos, las basales flojas, glabras a corta y esparcidamente pilosas, con los márgenes pestañosos; *lígulas* membranáceas, de 0.5 mm de largo, borde apical recto; seudolígula con pelos hasta de 4 mm de largo; cuello piloso; *láminas* linear-lanceoladas, de 5–22 cm de largo, 0.3–0.9 cm de ancho, planas, base atenuada o se continúan imperceptiblemente en su unión con la vaina y ápice acuminado, con la cara abaxial hirsuta y la adaxial glabra, los márgenes glabros. *Pedúnculos* 1–4 en la última vaina foliar, exertos a subincluidos, hasta de 30 cm de largo, filiformes, glabros; en ocasiones pedúnculos en los nudos medios. *Inflorescencias* terminales y axilares; racimos 1, raro 2, ascendentes, arquedos; eje principal ausente o de 1–1.5 cm de largo; pulvínulos glabros, ocasionalmente con una bráctea membranácea o un racimo rudimentario; raquis de los racimos de 4–7 cm de largo, 0.4–0.6 mm de ancho, triquetro, acanalado, glabro, terminando en una espiguilla desarrollada; pedicelos en pares, marcadamente desiguales, el de la espiguilla superior de 1.5–3 mm de largo y el de la espiguilla inferior ca. 0.3–1 mm, glabros, escabrosos; espiguillas en pares, no imbricadas, dispuestas en 1–2 series. *Espiguillas* largamente elipsoides, de 2–2.4 mm de largo, 1–1.1 mm de ancho, plano-convexas a levemente biconvexas, pubescentes, con pelos delgados y cortos, hasta de 0.3 mm de largo, distribuidos regularmente sobre gluma y lemma inferior o especialmente hacia el ápice y los márgenes; *gluma inferior* dimorfa: triangular y de ápice agudo, hasta de 1/4 del largo de la espiguilla, centrada, pubescente, especialmente hacia el ápice, enervia, en la espiguilla superior del par; lanceolada a acuminada, de 1/3–2/3 del largo de la espiguilla, generalmente centrada o levemente excéntrica, pubescente, 1-nervia, en la espiguilla inferior del par; *gluma superior* subigual a la lemma o levemente menor dejando libre el ápice del antecio, papirácea a hialina, no papilosa (se marcan las papilas del antecio), pubescente, 5-nervia, con un nervio central y los restantes próximos entre sí a equidistantes, raro el nervio medio ausente; *lemma inferior* tan larga como la espiguilla, superando levemente el ápice del antecio, plana a convexa, de ápice agudo, papirácea a hialina, no papilosa (se marcan las papilas del antecio), pubescente, 5–7-nervia, con un nervio central y los restantes próximos entre sí a equidistantes, los márgenes apenas doblados sobre el antecio. *Pálea inferior* y *flor inferior* ausentes; *antecio superior* elipsoide, de 1.9–2.1 mm de largo, 1 mm de ancho, plano-convexo, crustáceo, pajizo, lemma y pálea con células cuadradas, de paredes onduladas, con papilas simples distribuidas espaciadamente sobre la superficie, escasos pelos bicelulares y aguijones hacia el ápice de la lemma; lodículas de 0.3 mm de largo; estambres 3, anteras ca. 0.8 mm de largo. *Cariopsis* subelipsoide, de 1.3 mm de largo, 0.8 mm de ancho; hilo elíptico, 1/3 de la cariopsis; embrión 1/3–1/2 de la cariopsis.

Distribución y ecología. *Paspalum subfalcatum* es una especie poco coleccionada que crece en un área restringida al sur de Venezuela y norte de Brasil (Fig. 19), en selvas a lo largo de ríos sobre suelos arenosos o rocosos, entre los 80–130 m s.m.

Observaciones. Se caracteriza por sus espiguillas largamente elipsoides, pilosas, con pelos delgados y cortos, pedicelos marcadamente desiguales, gluma superior y lemma inferior papiráceas a hialinas, gluma inferior centrada en ambas espiguillas o levemente excéntrica en la espiguilla inferior, láminas de base atenuada, unidas imperceptiblemente con la vaina, lígula de 0.5 mm de largo.

Paspalum subfalcatum y *P. botterii* se asemejan por sus espiguillas pilosas; sin embargo, *P. subfalcatum* se diferencia por las espiguillas largamente elipsoides, plana-convexas a levemente biconvexas (vs. elipsoides a ligeramente obovoides y plano-convexas), la gluma y lemma papiráceas a hialinas (vs. membranáceas), los pedicelos marcadamente desiguales (vs. subiguales a desiguales) y la pre-

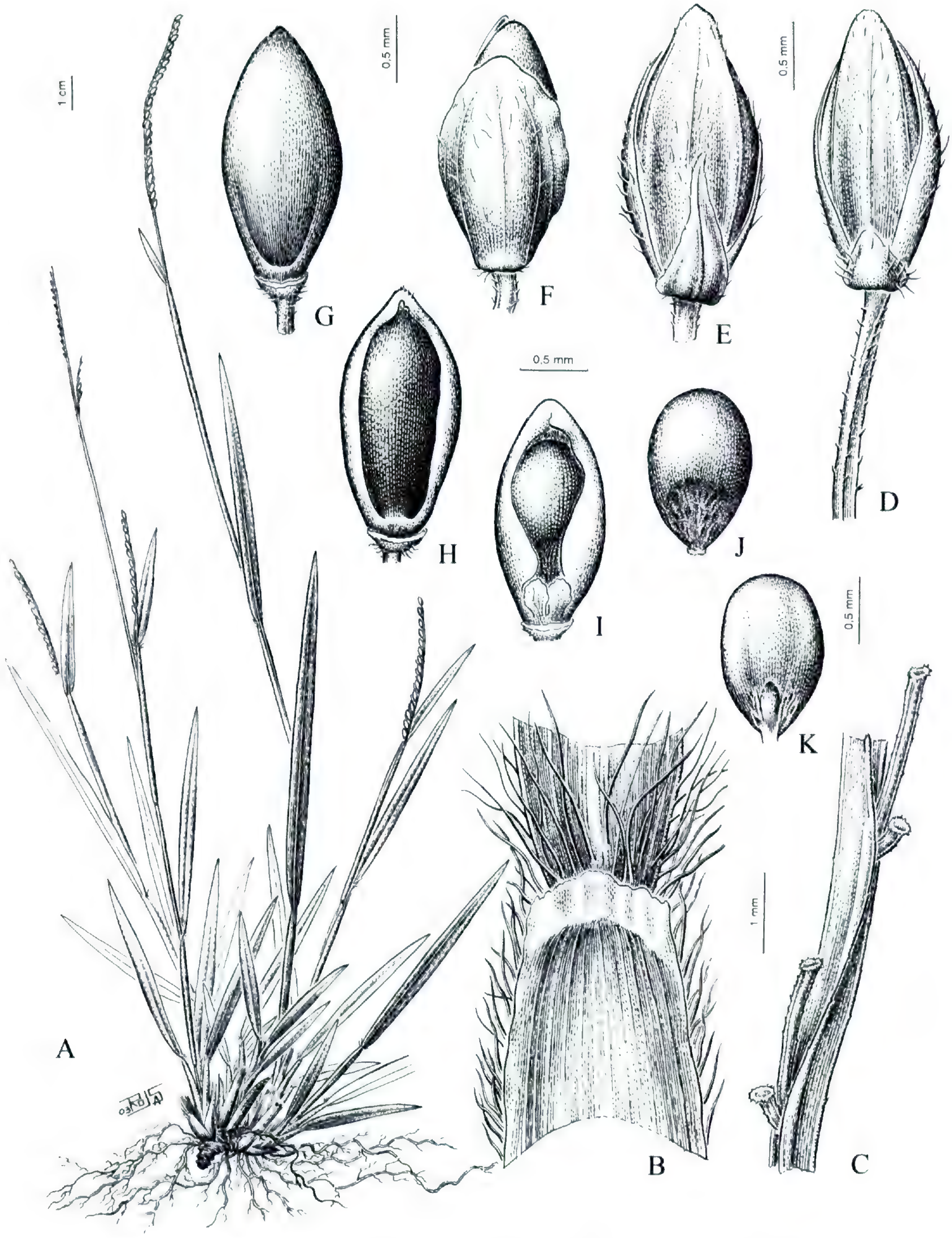

Figura 22. *Paspalum subfalcatum.* —A. Hábito. —B. Detalle de la lígula. —C. Porción del raquis de los racimos, pedicelos. —D. Espiguilla inferior, vista ventral mostrando la gluma inferior y lemma inferior. —E. Espiguilla superior, vista ventral mostrando la gluma inferior y lemma inferior. —F. Espiguilla, vista dorsal mostrando la gluma superior. —G. Antecio superior, vista dorsal mostrando la lemma superior. —H. Antecio superior, vista ventral mostrando la pálea. —I. Pálea superior, lodículas y cariopsis. —J. Cariopsis, mostrando el embrión. —K. Cariopsis, mostrando el hilo. (A–K, *Davidse 27842.*)

sencia constante de la gluma inferior, la cual es centrada en ambas espiguillas u ocasionalmente excéntrica en la espiguilla inferior (vs. ausencia o presencia de la gluma inferior).

Material estudiado. BRASIL. **Amazonas:** Río Negro, *Baldwin 3564* (US). VENEZUELA. **Amazonas:** Río Negro, on Río Baria, *Liesner 17160*/*** (MO, US); Río Negro, on Río Baría at mouth of Río Yatua, *Thomas et al. 3454* (MO); Río Negro, Río Pasimoni, betw. mouth and jct. with Río Baría and Río Yatua, *Davidse 27842* (MO, US).

36. Paspalum thrasyoides (Trin.) S. Denham, comb. nov. Basónimo: *Panicum thrasyoides* Trin., Gram. Panic.: 126. 1826. *Thrasya thrasyoides* (Trin.) Chase, Proc. Biol. Soc. Washington 24: 114. 1911. TIPO: Brasil. "Ubique in campis siccis," Dec. 1824, *G. H. von Langsdorff s.n.* (holotipo, LE-TRIN-983.03!, foto SI!; isotipos, MO-2180890 no visto, US!).

Referencias. Para descripción de la especie e ilustración de las espiguillas véanse Burman (1985 [1987]) y Chase (1911).

Distribución y ecología. Burman (1985 [1987]) cita a esta especie para cerrados y campos rupestres de Brasil central (Minas Gerais, Mato Grosso, Goiás y Distrito Federal); en el presente trabajo se agrega una colección para el estado de Pará. Renvoize (1998) cita a la especie para Bolivia, en Santa Cruz, La Paz y Beni (Fig. 19). Crece entre 200–1200 m s.m.

Observaciones. Véanse comentarios bajo *P. trinitense.*

Material estudiado. BRASIL. **Goiás:** 33 km S of Caiaponia, *Irwin & Soderstrom 7139*/*** (US). **Minas Gerais:** Serra do Curral, *Chase 8928* (US); Serra do Espinhao, *Hatschbach 27832* (US); Lagoa Santa, *Warming s.n.* (US-1125903); Santa Luzia, *Glaziou 20559* (US). **Pará:** Altos Tapajos, Río Cururú, *Anderson 10909* (US); sin estado, Río Branco, *Ule 8031* (US); sin estado, sin loc., *Sellow 1241* (US-1063671).

37. Paspalum trinitense (Mez) S. Denham, comb. nov. Basónimo: *Thrasya trinitensis* Mez, Repert. Spec. Nov. Regni Veg. 15: 125. 1918. TIPO: Trinidad y Tobago. Trinidad: Piarco Savanna, 25 Mar. 1893, *W. E. Broadway 5294* (holotipo, B no visto; isotipo, US-81807!).

Referencias. Para descripción de la especie e ilustración de las espiguillas véanse Burman (1985 [1987]) y Pohl (1980), respectivamente.

Distribución y ecología. Especie de amplia distribución que habita en Trinidad y Tobago, Belize, Honduras, Nicaragua, Colombia, Venezuela, British Guiana y Brasil (Fig. 12); crece en sabanas, pinares o campos arenosos, desde el nivel del mar hasta 1400 m de elevación.

Observaciones. Esta especie, como así también *P. huberi* y *P. thrasyoides,* presenta espiguillas con un callo en la base y la gluma superior más corta y más angosta que el antecio. Se diferencia de *P. huberi* por los raquis de los racimos pilosos (glabros en *P. huberi*); y de *P. thrasyoides* por presentar plantas más pequeñas (25–35 vs. 30–100 cm en *P. thrasyoides*) con cañas ramificadas (vs. simples en *P. thrasyoides*) y por el tamaño de las hojas (2–5 vs. 4–15 cm en *P. thrasyoides*), los racimos (1.5–6 vs. 4–12 cm en *P. thrasyoides*) y las espiguillas (2.4–2.6 vs. 3–4 mm en *P. thrasyoides*).

Material representativo estudiado. BELIZE. **Toledo:** SW of Mango Creek, *Russell 1145* (US). COLOMBIA. **Meta:** Fundation Yamato, rd. Puerto Lopez–Puerto Gaitan, *Laegaard & Mayorga 17602* (SI). **Vichada:** San José de Ocuné, *Hermann 11095* (US). BRITISH GUIANA. Basin of Rupununi River, *Smith 2410* (US). HONDURAS. **Gracias a Dios:** La Mosquitia, orilla Río Dursuna, *Nelson & Vargas 5039* (MO). **Olancho:** vaguada Río de Culmí, *Nelson & Romero 4673* (MEXU). NICARAGUA. **Zelaya:** 47 km rd. from Puerto Cabezas to Rosita, *Stevens 8589* (US). TRINIDAD Y TOBAGO. **Trinidad:** Savana Aripo, *Soderstrom 981*/*** (US). VENEZUELA. **Apure:** Pedro Camejo, *Davidse & Gonzalez 14261* (US). **Bolívar:** Gran Sabana, *Zuloaga et al. 4422* (SI, VEN).

38. Paspalum unispicatum (Scribn. & Merr.) Nash, N. Amer. Fl. 17: 193. 1912. *Panicum unispicatum* Scribn. & Merr., Bull. Div. Agrostol., U.S.D.A. 24: 14. 1901. TIPO. México. Oaxaca: valley of Oaxaca, 13 Jul. 1891, *C. G. Pringle 6717* (holotipo, US!; isotipos, MO-2977107!, P!, W no visto). Figura 23.

Plantas perennes, rizomatosas, rizomas con zonas de entrenudos alargados, delgados, arqueados, cubiertos por numerosos catáfilos agudos, coriáceos, lustrosos, glabros a corta y densamente pilosos; *cañas* de 30–90 cm de alto, 0.2–0.3 cm de diámetro, erectas, simples o en ocasiones ramificadas en los nudos basales; entrenudos de 7–14 cm de largo, los inferiores próximos, de 3–5 cm de largo, pajizos, glabros; nudos glabros, castaños. *Vainas* de 5–16 cm de largo, superpuestas hacia la base, aquilladas, glabras o esparcidamente papiloso-pilosas hacia la porción distal, con pelos tuberculados, caducos, a hirsutas, con un margen pestañoso, el restante glabro; *lígulas* membranáceas, de 3–4 mm de largo, de ápice lacerado, castañas; seudolígula formada por un mechón de pelos de 3–7 mm de largo; lígula externa comúnmente presente, membranácea, de 1 mm de largo; cuello glabro a cortamente piloso; *láminas* linear-lanceoladas, de 10–30 cm de largo, 0.5–1.6 cm de ancho, reduci-

Figura 23. *Paspalum unispicatum.* —A. Hábito. —B. Detalle de la lígula. —C. Porción del raquis de los racimos, pedicelos. —D. Espiguilla inferior, vista ventral mostrando la gluma inferior y lemma inferior. —E. Espiguilla inferior, vista dorsal mostrando la gluma superior. —F. Pálea inferior, con lodículas y estambres. —G. Antecio superior, vista dorsal mostrando la lemma. —H. Antecio superior, vista ventral mostrando la pálea. —I. Pálea superior y lodículas. (A–I, *Cabrera 27534.*)

das hacia el ápice de las cañas, herbáceas, planas a plegadas, pajizas, ascendentes, de base redondeada a subcordada y ápice agudo a largamente agudo, esparcidamente papiloso-pilosas en ambas caras a glabras, los márgenes pilosos, largamente pestañosos hacia la base. *Pedúnculos* 1–2(3) en la última vaina foliar, exertos a subincluidos, hasta de 32 cm de largo, cilíndrico-acanalados, glabros. *Inflorescencias* terminales y axilares; racimos 1, raro 2, ligeramente arqueados a rectos; eje principal ausente o hasta de 2 cm de largo, aplanado, glabro; pulvínulos glabros a largamente pilosos; raquis de los racimos de 4–18 cm de largo, 0.5–0.8 mm de ancho, triquetro, acanalado, glabro, con los márgenes escabriúsculos, con pelos aislados en los márgenes, terminando en una espiguilla desarrollada; pedicelos en pares, desiguales, el de la espiguilla superior hasta de 1.2 mm de largo, hispídulos; espiguillas imbricadas, dispuestas en 4 series apretadas. *Espiguillas* obovoides a anchamente elipsoides, de 2.8–3.6(–3.9) mm de largo, 1.6–1.8 mm de ancho, ligeramente cóncavo-convexas, de ápice agudo a cortamente mucronado, pajizo-verdosas, glabras; *gluma inferior* dimorfa: ancha y de ápice obtuso a agudo, 1/4–1/3 del largo de la espiguilla, centrada, glabra, enervia, en la espiguilla superior del par; ovado-acuminada, hasta 3/4 del largo de la espiguilla, excéntrica, glabra, 1-nervia, el nervio conspicuo y escabroso hacia el ápice, en la espiguilla inferior; a veces de morfología variable incluso en el mismo racimo; *gluma superior* tan larga como la espiguilla o, en ocasiones, dejando al descubierto el ápice del antecio, ápice comúnmente mucronado, no papilosa, 5-nervia, con un nervio central marcado o carinado y los marginales próximos entre sí; *lemma inferior* glumiforme, tan larga como la espiguilla, lisa a finamente papilosa, cartácea, con el dorso usualmente sulcado, 5–7-nervia, con un nervio central y los marginales próximos entre sí a equidistantes, los márgenes doblados sobre el antecio; *pálea inferior* anchamente elíptica, tan larga como su correspondiente lemma, hialina, los nervios más o menos endurecidos; *flor inferior* estaminada, estambres 3, anteras de 1.6 mm de largo; *antecio superior* anchamente elípsoide, de 2.4–3.4(–3.7) mm de largo, 1.3–1.5 mm de ancho, plano-convexo a ligeramente cóncavo-convexo, crustáceo, pajizo, lemma y pálea con células cuadradas, de paredes onduladas, con papilas verrugosas distribuidas regularmente sobre la superficie, centradas en las células, con 5–6 verrugas cada una; lodículas de 0.4 mm de largo; estambres 3, anteras de 1.2 mm de largo, castañas. *Cariopsis* anchamente elipsoide, de 1.6–2 mm de largo, 1.2–1.3 mm de ancho; hilo anchamente elíptico, 1/3 de la cariopsis, embrión 1/3–1/2 de la cariopsis.

Números cromosómicos. $n = 20$ (Davidse & Pohl, 1974), $2n = 40$ (Saura, 1941).

Distribución y ecología. Crece en México, Honduras, Cuba y norte de Venezuela, luego es muy frecuente desde Bolivia a Argentina y Uruguay, se encuentra también en Minas Gerais, Brasil. Jørgensen y León-Yánez (1999) citan a esta especie para Loja, Ecuador, mientras que Beetle et al. (1999) la citan para Texas, Estados Unidos de América (Fig. 8). Habita en bosques secos y campos de altura, en bordes de caminos, vías, invadiendo jardines; en suelos arenosos, arcillosos o modificados; entre 250–1670 m s.m. Especie forrajera poco productiva (Rosengurtt et al., 1970; Mejía Saulés & Dávila Aranda, 1992).

Observaciones. *Paspalum unispicatum* se caracteriza por sus rizomas alargados, cubiertos por catáfilos, las cañas generalmente son simples y con inflorescencias sólo en el nudo terminal, cada inflorescencia presenta 1, raro 2, racimos; es característica también la presencia de una lígula externa. Las espiguillas son obovadas a anchamente elipsoides, la gluma inferior es usualmente dimorfa y la gluma superior mucronada, con el nervio medio marcado a carinado.

En los ejemplares *Rojas 2313* y *Anderson 1179* se observaron cilias en los márgenes apicales de la gluma superior de varias espiguillas.

Chase (1929) menciona que la especie es frecuentemente afectada por hongos que alteran las inflorescencias.

Especie afín a *Paspalum pilosum* y a *P. monostachyum*. La relación con *P. monostachyum* se discute bajo esta última especie. *Paspalum pilosum* se diferencia de *P. unispicatum* por presentar rizomas cortos, cañas simples o ramificadas en los nudos medios, lígula más corta (de 1–2 mm), cuello densamente piloso, sin lígula externa, pedúnculos 1–4, raquis de los racimos de 0.8–1.5 mm de ancho, espiguillas más pequeñas, de (2.2–)2.4–3 mm de largo y 1.5–1.8 mm de ancho y lemma inferior papilosa.

Material representativo estudiado. ARGENTINA. **Buenos Aires:** Isla Martín García, camino del monumento al Arenal central, *Hurrell et al. 1570* (SI). **Catamarca:** Del Alto, *Venturi 7194* (SI). **Chaco:** 1° de Mayo, Colonia Benítez, *Schulz 18072* (SI). **Córdoba:** sin loc., *Sturkert 367** (SI). **Corrientes:** Mercedes, *Millán 415* (SI). **Entre Ríos:** Colón, San José, *Zucol 586* (SI). **Formosa:** Comandante Fontana, Enrique Urién, *Schulz 3107* (G). **Jujuy:** Dr. Manuel Belgrano, *Zuloaga & Deginani 3621*** (SI). **La Rioja:** Gobernador Gordillo, *Nicora 18526* (SI). **Salta:** Anta, Pozo Largo, 10 km al SSE de J. V. González, *Saravia Toledo 1224* (SI). **San Luis:** San Martín, Guanaco

Pampa, *Baez 12* (BAA). **Santa Fe:** Capital, Recreo, *Achenbach 109* (LIL). **Santiago del Estero:** C. Pellegrini, Estancia El Remate, *Venturi 5717* (LIL, MO, SI, US). **Tucumán:** Burruyacú, El Timbó, *Venturi 2395* (LIL, SI, US). BOLIVIA. **Chuquisaca:** Luis Calvo, zona central, *Pensiero & Marino 4457* (MO). **Santa Cruz:** 2 km W of Pampa Grande, *Renvoize & Cope 4055* (MO). BRASIL. **Minas Gerais:** Serra do Cipó, *Pires & Black 2722* (US). CUBA. **Pinar del Río:** Mendoza, railroad station, *Ekman 11457* (G). **Villa Clara:** 30 km E of Trinidad, *Ekman 13957* (G). HONDURAS. **Choluteca:** Marcovia, *Mejía 9* (MO). **Francisco Morazán:** Loma Linda Norte, Tegucigalpa, *Paz 30* (MEXU). MÉXICO. **Nuevo León:** Monterrey, *Hitchcock 931* (MO). **Tamaulipas:** 4 mi. S of Jaumave, *Stanford et al. 2315* (MO). PARAGUAY. **Alto Paraguay:** Pto. Pinusco, *Anderson 1179* (US); Pto. Casado, barrancas Río Paraguay, *Rojas 2313* (SI, US). **Boquerón:** Cerca de Teniente Rueda, a 30 km de Mariscal Estigarribia, *Ramírez 605* (CTES). **Concepción:** Col. San Lázaro, Río Apa, *Rojas 5474* (US). **Guairá:** San Salvador, *Rojas 2743* (US). **Presidente Hayes:** Estancia Loma Pyta, *Arenas s.n.* (BACP673, CTES). URUGUAY. **Paysandú:** Río Uruguay y Chapicuy, *Rosengurtt B–3253* (US). VENEZUELA. **Aragua:** Maracay, Facultad de Agronomía, *Cárdenas 88* (MO). **Distrito Federal:** 2 km NW of Carayaca by rd., *Davidse 2891* (MO, US). **Yaracuy:** Bureche, cerca de Barquisimeto, *Burkart 16491* (SI).

39. Paspalum variabile (E. Fourn.) Nash, N. Amer. Fl. 17(2): 180. 1912. *Dimorphostachys variabilis* E. Fourn., Mexic. Pl. 2: 15. 1886. TIPO: México. *A. B. Ghiesbreght s.n.* (lectotipo, designado por Chase (Contr. U.S. Natl. Herb. 28: 108. 1929), P!, foto SI!; isotipo, US-865865!). Figura 24.

Dimorphostachys ghiesbreghtii E. Fourn., Mexic. Pl. 2: 16. 1886. TIPO: México. *A. B. Ghiesbreght s.n.* (holotipo, P!, foto SI!).

Dimorphostachys schaffneri E. Fourn., Mexic. Pl. 2: 15. 1886. *Panicum schaffneri* (E. Fourn.) Kuntze, Revis. Gen. Pl. 3(3): 358. 1898. *Paspalum schaffneri* (E. Fourn.) Scribn., Publ. Field. Columbian Mus., Bot. Ser. 2(1): 24. 1900. TIPO: México. Mirador, *J. G. Schaffner s.n.* (lectotipo, designado por Chase (Contr. U.S. Natl. Herb. 28(1): 107. 1929), P!, foto SI!; isotipo, US-865862!).

Plantas perennes, cespitosas, rizomas de entrenudos cortos; *cañas* erectas, de 70–100 cm de alto, 1.8–2.1 mm de diámetro, simples, en ocasiones ramificadas en los nudos medios; entrenudos de 9–22 cm de largo, los inferiores más cortos, estriados, cilíndricos a ligeramente comprimidos, glabros; nudos glabros, castaños. *Vainas* de 5–20 cm de largo, usualmente más cortas que los entrenudos, flojas, aquilladas, estriadas, de superficie glabra y márgenes membranáceos y pestañosos; *lígulas* membranáceas, hasta de 2 mm de largo, ápice lacerado; seudolígula con escasos pelos de 4–5 mm de largo; cuello castaño, glabro a piloso; *láminas* lanceoladas, de 10–30 cm de largo, 0.7–1.8 cm de ancho, planas, de base redondeada a angostada y ápice acuminado, nervio medio aquillado, pubescentes o glabras en las superficies y los márgenes pestañosos, escabrosos. *Pedúnculos* 1–3 en la última vaina foliar, exertos a subincluidos, hasta de 20 cm de largo, glabros; usualmente 1 pedúnculo incluido a parcialmente exerto en las vainas subapicales. *Inflorescencias* terminales y axilares; racimos 2–4, alternos, solitarios en las inflorescencias subapicales; eje principal de 2–6 cm de largo, glabro; pulvínulos glabros a escasamente pilosos; raquis de los racimos de 3–9 cm de largo, 0.9–1.2 mm de ancho, ascendente, triquetro, aplanado, acanalado, glabro, terminando en una espiguilla desarrollada; pedicelos en pares, escabrosos, glabros, desiguales, el de la espiguilla superior hasta de 1.4(–2) mm de largo; espiguillas imbricadas, dispuestas en 2–4 series sobre el raquis. *Espiguillas* elipsoides a ligeramente obovoides, de 2.9–3.2 mm de largo, 1.6–1.9 mm de ancho, plano-convexas, pubescentes hacia los márgenes, con pelos delgados, cortos, hasta de 0.3 mm de largo o glabras, maculadas a la madurez; *gluma inferior* dimorfa: subtriangular, de 1/4–1/2 del largo de la espiguilla, centrada, comúnmente con un amplio margen hialino, castaño o pajizo, ciliado, 2-nervia, comúnmente con los nervios confluentes en el ápice, en la espiguilla superior del par; lanceolada, de ápice acuminado, 1/3–4/5 del largo de la espiguilla, excéntrica, con un margen hialino angosto, pubescente, 3-nervia, con el margen central escabroso, en la espiguilla inferior del par; *gluma superior* tan larga como la espiguilla o ligeramente más corta, no papilosa, la superficie pubescente especialmente hacia los márgenes, 5-nervia, con un nervio central y los restantes marginales, próximos entre sí a equidistantes; *lemma inferior* tan larga como la espiguilla, con el ápice agudo a apiculado, plana a apenas sulcada, no papilosa, especialmente pubescente hacia los márgenes, 5-nervia, con un nervio central y los restantes marginales, próximos entre sí a equidistantes, con los márgenes doblados sobre el antecio; *pálea inferior* y *flor inferior* ausentes; *antecio superior* anchamente elipsoide a obovoide, de 2.3–2.4 mm de largo y 1.4–1.6 mm de ancho, plano-convexo, crustáceo, pajizo a ferrugíneo, lemma y pálea con células cuadradas, de paredes onduladas, con papilas verrugosas regularmente distribuidas, centradas, con 4–5 verrugas cada una, micropelos hacia el ápice de lemma y pálea, con la célula apical 2 veces más larga que la basal; lodículas de 0.3–0.4 mm de largo; estambres no vistos. *Cariopsis* subcircular, de 1.5–1.6 mm de largo, 1.3 mm de ancho; hilo elíptico, 1/3 de la cariopsis; embrión 1/4–1/3 de la cariopsis.

Figura 24. *Paspalum variabile.* —A. Hábito. —B. Detalle de la lígula. —C. Porción del raquis de los racimos, pedicelos. —D. Espiguilla inferior, vista ventral mostrando la gluma inferior y lemma inferior. —E. Espiguilla superior, vista ventral mostrando la gluma inferior y lemma inferior. —F. Espiguilla, vista dorsal mostrando la gluma superior. —G. Antecio superior, vista dorsal mostrando la lemma. —H. Antecio superior, vista ventral mostrando la pálea. —I. Pálea superior, lodículas y cariopsis. —J. Cariopsis, mostrando el embrión. —K. Cariopsis, mostrando el hilo. (A–K, *Hitchcock 6439.*)

Nombres vulgares. "camalote," "camalotillo" (Beetle et al., 1999, México).

Número cromosómico. $2n = 40$ (Morrone, inéd.).

Distribución y ecología. Crece en México, en los estados de Hidalgo, Puebla, Veracruz, Oaxaca y Chiapas. Chase (1929) y Hitchcock (1930) citan colecciones para Costa Rica y Chase (1929) para el estado de Morelos, en México. Pohl y Davidse (1994) cita la especie para México a Honduras (Fig. 15). Crece en bosques o claros, en bordes de ríos o sobre suelos arcillosos, es frecuente en cafetales, entre 800–1560 metros de altura.

Observaciones. Es característica de la especie la gluma inferior 2-nervia, con un amplio margen hialino, castaño o pajizo en la espiguilla superior del par.

Paspalum variabile se asemeja a *P. botterii* por la pilosidad y máculas en las espiguillas, pero ambas se diferencian por el tamaño de las espiguillas (2–3 mm de largo y 1.2–1.4 mm de ancho en *P. botterii* vs. 2.9–3.2 mm de largo y 1.6–1.9 mm de ancho en *P. variabile*), la gluma inferior siempre presente, 2-nervia y con un amplio margen hialino, castaño o pajizo en la espiguilla superior del par, en *P. variabile*.

Material representativo estudiado. MÉXICO. **Chiapas:** 4 mi. N of Jitopol on rd. to Pueblo Nuevo Solistahuacan, *Breedlove 12045* (US). **Hidalgo:** about Lake Atexca below Molango, *Moore 3487* (US). **Oaxaca:** San Jerónimo, *Zuloaga et al. 7397* (SI). **Puebla:** Huauchinango, *Aragón 192* (MEXU). **Veracruz:** Córdoba, *Hitchcock 6439*/*** (US).

Especie Excluida

Paspalum glabrinode (Hack.) Morrone & Zuloaga, Darwiniana 29(1–4): 262. 1989. *Panicum glabrinode* Hack., Ann. Cons. Jard. Genève 17: 284. 1914. *Brachiaria glabrinodis* (Hack.) Henrard, Blumea 3: 435. 1940. TIPO: Argentina. Misiones: Santa Ana, 14 Jan. 1913, *H. Rodríguez 721* (holotipo, W no visto; isotipos, BA no visto, BAA no visto, BAF no visto, LIL no visto, SI!, US-1817349!, US-80753!).

Morrone y Zuloaga (1989) relacionan a esta especie con el grupo Decumbentes de *Paspalum* por presentar la gluma inferior dimorfa en el par de espiguillas. Sin embargo, esta especie es aquí excluida del subgénero *Harpostachys* sobre la base del número de racimos por inflorescencia (12–40 racimos), la ausencia de inflorescencias axilares en la última vaina foliar y por la presencia de pelos urticantes en la porción distal de las vainas foliares.

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Apéndice 1. Lista de Especies Aceptadas en *Paspalum* Subgénero *Harpostachys* (Trin.) S. Denham.

1. **Paspalum achlysophilum** (Soderstr.) S. Denham [= *Thrasya achlysophila* Soderstr.]
2. **Paspalum adoperiens** (E. Fourn.) Chase
3. **Paspalum altsonii** Chase
4. **Paspalum auricomum** (A. G. Burm.) S. Denham [= *Thrasya auricoma* A. G. Burm.]
5. **Paspalum axillare** Swallen [= *Thrasya axillaris* (Swallen) A. G. Burm. ex Judz.]
6. **Paspalum botterii** (E. Fourn.) Chase
7. **Paspalum campylostachyum** (Hack.) S. Denham [= *Thrasya campylostachya* (Hack.) Chase]
8. **Paspalum carajasense** S. Denham [= *Thrasya longiligulata* C. N. Bastos & A. G. Burm.]
9. **Paspalum cinerascens** (Döll) A. G. Burm. & C. N. Bastos
10. **Paspalum crucense** (Killeen) S. Denham [= *Thrasya crucensis* Killeen]
11. **Paspalum cultratum** (Trin.) S. Denham
12. **Paspalum decumbens** Sw.
13. **Paspalum dispar** Chase
14. **Paspalum calliferum** S. Denham [= *Thrasya robusta* Hitch. & Chase]
15. **Paspalum foliiforme** S. Denham [= *Thrasya petrosa* (Trin.) Chase]
16. **Paspalum glaziovii** (A. G. Burm.) S. Denham [= *Thrasya glaziovii* A. G. Burm.]
17. **Paspalum graniticum** (A. G. Burm.) S. Denham [= *Thrasya granitica* A. G. Burm.]
18. **Paspalum hintonii** Chase
19. **Paspalum huberi** S. Denham [= *Thrasya stricta* A. G. Burm.]
20. **Paspalum inconstans** Chase
21. **Paspalum monostachyum** Vasey
22. **Paspalum mosquitiense** (Davidse & A. G. Burm.) S. Denham [= *Thrasya mosquitiensis* Davidse & A. G. Burm.]
23. **Paspalum nutans** Lam.
24. **Paspalum oreophilum** (A. G. Burm.) S. Denham [= *Thrasya oreophila* A. G. Burm.]
25. **Paspalum orinocense** S. Denham [= *Thrasya paspaloides* Kunth]
26. **Paspalum parvulum** (A. G. Burm.) S. Denham [= *Thrasya parvula* A. G. Burm.]
27. **Paspalum peckii** F. T. Hubb.
28. **Paspalum petilum** Chase
29. **Paspalum pilosum** Lam.
30. **Paspalum procerum** S. Denham [= *Thrasya hitchcockii* Chase]
31. **Paspalum scandens** Tutin [= *Thrasya scandens* (Tutin) Soderstr. & A. G. Burm.]
32. **Paspalum schumannii** (Pilg.) S. Denham [= *Thrasya schumannii* (Pilg.) Pilg.]
33. **Paspalum seminudum** (A. G. Burm.) S. Denham [= *Thrasya seminuda* A. G. Burm.]
34. **Paspalum setosum** (Swallen) S. Denham [= *Thrasya setosa* Swallen]
35. **Paspalum subfalcatum** (Döll) Tutin
36. **Paspalum thrasyoides** (Trin.) S. Denham [= *Thrasya thrasyoides* (Trin.) Chase]
37. **Paspalum trinitense** (Mez) S. Denham [= *Thrasya trinitensis* Mez]
38. **Paspalum unispicatum** (Scribn. & Merr.) Nash
39. **Paspalum variabile** (E. Fourn.) Nash

Apéndice 2. Índice de Colecciones.

Índice de colecciones en orden alfabético del material estudiado del subgénero *Harpostachys* de *Paspalum*. Cada espécimen es citado por el apellido del primer colector. Se indica entre paréntesis el número de la especie (vease Apéndice 1). De *Paspalum peckii* sólo se observó el ma-

terial tipo. De *P. achlysophilum*, *P. parvulum*, *P. schumannii* y *P. seminudum* no se observó material. Con un asterisco (*) se señalan los ejemplares utilizados para estudios histofoliares y con dos asteriscos (**) los utilizados para estudios de antecios superiores.

Abraham 30 (6), *346* (12); *Achenbach 109* (38); *Acosta Solís 12154* (12); *Adams 7609* (12); *Ahumada 6234* (38); *Alain 36770* (12); *Allard 20613* (12) *21155* (12), *21595* (12); *Alvarez 413-a* (6); *Anderson 1020* (12), *1179* (38), *9774*/** (15), *10187* (12), *10697* (12), *10782* (15), *10909* (36), *35721* (23), *36112* (29); *Andino 97* (29); *Andrade 1314* (23), *s.n.* (12); *Antonio 2241* (12); *Aragón 192* (39); *Archer 468* (20), *1279* (20), *1617* (20), *1910* (12), *2134*** (12), *2752* (12); *Arenas s.n.* (38); *Asplund 5598* (12), *5834* (12), *8537* (12), *8838* (23), *8975* (12), *10623* (20), *13183* (12); *Atwood 1272* (6); *Avella Martínez E74* (6); *Ayala 1928* (12), *5923* (12); *Aymard 3666* (12), *4797* (29), *7372* (12), *8069* (12).

Bacigalupo 1632 (38); *Baez 12* (38); *Baldwin 3564* (35); *Barkly 130** (20); *Bartlett 10407* (6); *Beck 4880* (20), *14940* (7), *17193* (7), *18538* (29), *25183* (20); *Beetle M–1174* (6); *Benavides 9995* (12); *Bentacur 356* (12), *375* (12); *Berry 506* (29); *Black 1819** (12), *2852* (12), *2960* (12), *48–3055* (12), *54–16961* (23), *17059* (14); *Blas 148* (6); *Blum 1739* (23); *Boechat s.n.* (12); *Boege 223* (39), *2495* (2); *Bourgeau 1658* (39), *2598* (39); *Brant 1629* (23); *Bravo 11* (6); *Breedlove 10037* (6), *11035* (39), *12045* (39), *38572* (29); *Breglia 88* (38); *Bristol 933* (20), *967* (20); *Britton 1249* (23), *1582* (12), *2135* (12), *4118* (12); *Brizuela 674* (38); *Broadway 261* (23), *876* (23), *5313* (23), *5331* (23), *5802* (12), *8030* (12); *Buchtien 14* (29), *47/2* (20), *84* (12), *416* (20), *1161* (12), *5314* (12), *6445* (12), *7105* (12), *7106* (13), *7109* (20), *7111* (20), *s.n.* (12); *Burandt VO138* (7), *V0159* (6); *Burkart 7196* (38), *10221* (38), *13334* (38), *13863* (38), *16291* (15), *16491* (38), *16630*** (6), *17079* (15), *20148* (38), *20661* (38), *23258* (38), *25253* (38), *25315* (38), *25316* (38); *Bush 264* (6); *968* (6); *Buting 7280* (12).

Cabrera 27292 (38), *27534* (38); *Calderon 1238* (6); *Calónico 15707* (6); *Cárdenas 88* (38); *Cardona 2966* (28); *Carranco 791* (6); *Castillo Campos 14415* (6); *Catalán 123* (6); *Chaffanjon 280** (25); *Chase 932* (6), *1844* (11), *6235* (12), *7165* (6), *7479* (6), *7638* (23), *7731* (23), *7788* (6), *7822* (6), *7860* (29), *7890* (29), *8025* (29), *8199* (23), *8341* (23), *8346* (29), *8651** (11), *8671* (11), *8928* (36), *8972* (11), *8999* (12), *9120* (23), *9199* (23), *9448* (23), *9510* (12), *9512* (23), *9974* (12), *10046* (23), *10229* (11), *10844*** (9), *10931* (9), *11473* (15), *11489* (12), *11493* (12), *11677* (9), *12000* (12), *12314* (23), *12349* (6), *12403* (30), *12569* (12), *19636* (23), *71121/2* (6); *Chavelas 13* (6), *16* (6), *25* (6); *Chazaro 159* (6); *Chevez 10* (29); *Cisneros 155* (6); *Clayton 4104* (29), *4760* (12), *4868a* (15); *Clotter 11* (6); *Contreras 1109* (6), *1155* (6); *Conzalli 1160* (6); *Cook 289* (7); *Cooley 9055* (21); *Corona 11* (6); *Cory 45679* (21); *Couret 171* (28); *Cowan 1306* (12), *1365* (12), *1821* (31), *2215* (28), *3249* (29); *Cremers 7685* (12), *9689* (12), *12348* (9); *Croat 23700* (6), *23828* (6), *24702* (6), *27212* (12), *39465* (39), *52033* (12), *58927* (12), *62270* (12), *63676* (2); *Cuatrecasas 7521* (23), *21036* (12), *21041* (12), *21423* (12), *22549* (20); *Cuezzo 11141* (38); *Curti 327* (12).

da Silva 235 (29), *280* (23), *1854* (29), *5034* (15); *Davidse 2468* (23), *2626* (13), *2682* (12), *2743*** (25), *2891* (38), *2917* (29), *3020* (23), *4515* (30), *4754** (14), *5217* (12), *5556* (29), *5635* (12), *10137*** (14), *10609* (29), *11366* (23), *11416* (23), *11516* (29), *14261* (37), *15532* (12), *16795* (29), *17141* (29), *17479* (29), *19136* (30), *19389* (29), *19794*** (29), *20146* (6), *20195* (6), *20273* (6), *20293* (6), *20353* (6), *20421* (6), *20459* (6), *20907* (12), *21503* (12), *21533* (23), *21725* (23), *22425* (23), *22499* (12), *22606* (28), *22781* (23), *23441* (29), *26655* (29), *26920* (12), *27022* (3), *27025* (28), *27793* (12), *27842* (35), *29739* (6), *31554* (29), *32492*/** (7), *32637* (6), *34493* (12), *35480* (2), *35920* (12); *de Granville 8294* (12); *de la Cruz 3868* (12); *Deginani 863* (38); *Delascio 12268* (23); *Diggs 2794* (39); *Dodge 17352* (23); *Dodson 7974* (12); *Dorr 5399* (12); *Droege 228* (2), *232* (6); *Drumont 112* (38); *Duarte 5068* (11); *Duke 7570* (12); *Dusén 13507* (29), *14925* (29); *Du 4059* (23); *Dwyer 2563* (29), *2563A*** (30), *15246* (12).

Edwards 151 (28); *Egler 1473* (9); *Eiten 6066* (23); *Ekman 934* (6), *2376* (6), *3483* (12), *5948* (6), *9014* (12), *11038* (12), *11095* (13), *11255* (13), *11435* (12), *11457* (38), *11497* (6), *11595* (13), *11709* (12), *13426** (13), *13928* (13), *13957* (38); *Ernst 1117* (23), *2067* (23); *Espinal 24* (6); *Espinoza 160* (6); *Evans 2988* (3).

Faett 25602 (20); *Febres 4* (3); *Fendler 2535* (12); *Fernandez 5240* (3), *7420* (12); *Ferreyra 17178* (12), *17247* (12); *Filgueiras 2016* (29), *2052* (15), *2101* (29), *2104* (29), *2119* (15), *2193*** (16), *2219* (29); *Flores 4136* (6); *Forero 5117* (29); *Fortunato 1310* (38); *Froés 20563* (12).

Galván 304 (6), *425* (6), *477* (6); *Gamía 4431* (20), *4587* (12); *García 10985* (12); *Gardner 3496* (29), *3508* (9); *Garnier 810* (6); *Gasche 109* (12); *Gentle 6249* (12), *6806* (6), *6882* (6), *7416* (12), *8790* (6), *9229* (12); *Gentry 337* (6), *16846* (23), *20092* (12), *28909* (12), *29469* (12); *Geyskes 68* (12); *Giardelli 1005* (38); *Giraldo-Cañas 2594* (15), *2716* (12); *Glaziou 20559* (36), *20562* (11), *22433* (16), *22434* (29), *22435* (9), *22436* (15), *22483* (16), *22579* (29); *Goeldi 40* (23); *Goll 90* (6); *González 598* (29), *1187* (12); *Goodland 455* (23); *Gould 10896* (13), *12568* (6); *Grant 779* (6); *Granville 9333* (31), *11838* (9), *12240* (9); *Grasel 10027* (12); *Grayum 4256** (6), *6775* (12); *Grignon 84277* (20); *Groger 528* (34); *Guanchez 4844* (25); *Guzmán 694* (6), *1082* (6).

Haber 9600 (6), *11281* (12); *Hahn 4516* (31), *5252* (28); *Hamilton 382* (12); *Hammel 3373* (12), *5506* (29); *Harley 11221* (9), *11227* (9), *15330* (29), *17387* (29); *Harmon 3690* (29), *3804* (6); *Harris 11606* (12); *Hartley SH 140* (38); *Hatschbach 2256* (23), *8813* (9), *27832* (36), *42908* (29), *44577* (23); *Heath 1118* (2); *Heithaus 171* (6); *Heller 6354* (12); *Hermann 11095* (37); *Hernandez 182* (6), *1117* (6), *3372* (6); *Herrera 7* (6); *Hill 12801* (12); *Hinton 4515* (6), *5206* (6); *Hitchcock 930* (12), *931* (38), *935* (39), *5573* (6), *5760* (6), *6209* (6), *6323* (39), *6377* (6), *6411* (39), *6439*/** (39), *6608* (39), *6826* (6), *7962* (12), *7988* (7), *8047* (23), *8130* (29), *8192* (29), *8606* (6), *8630 1/2* (6), *8681* (6), *8686* (6), *8724* (6), *8744* (6), *8956* (6), *9079* (6), *9097* (2), *9553* (12), *9957* (23), *9987* (29), *10075* (29), *10189* (29), *10299* (23), *17034* (23), *17083* (23), *17195* (12), *17421* (12), *19909* (29), *20413* (12), *21189* (20), *21204* (20), *22061* (12), *22066* (12), *22605* (20), *22609* (20), *22694* (7), *22718* (12), *22728* (7), *22734* (20), *s.n.* (12); *Hoehne 9854* (9); *Hoff 6504* (9); *Hoffman 3057* (28); *Holst 2599* (25); *Hoock 571* (9), *804* (31), *1016* (14), *1300* (23), *1302* (12); *Hoover 3027* (12); *Howell 10227* (6); *Huber 1281* (34), *4752*/** (34), *7831* (29), *11845* (15), *59332* (28); *Humbert 27237* (12); *Hunziker 1638* (38); *Hurrell 1570* (38).

Irwin 7139/** (36), *8504* (12), *9529* (29), *9650* (29), *10196* (12), *10652* (29), *10831* (12), *10892* (29), *11259* (9), *11889* (12), *12076* (9), *12994** (9), *13764*** (29), *15348** (16), *16287* (12), *16337* (9), *18610* (29), *19003*

(29), *24239* (29), *27989*/*** (24), *29335*** (11), *34469* (9); *Izaguirre 148* (29).

Jansen-Jacobs 690 (3), *1231* (3), *1562* (12); *Jenman 7817* (12); *Johnston 217* (23), *1225* (23).

Killeen 1819/*** (10), *5451* (29), *5645* (9); *Killip 6002* (12), *14367* (6), *15112* (29), *15143* (20), *22528* (29), *25387* (12), *25468* (12), *27361* (12), *30432* (23), *34763* (12); *Klein 10374*** (23), *10754* (23), *11702* (12), *11717* (12); *Knapp 3703* (12); *Kral 27529* (18), *69239* (37); *Kuhlmann 1767* (9).

Laegaard 17484 (15), *17505* (15), 17572 (19), *17583* (15), *17602* (37); *Laínez 93* (2); *Landing 662* (12); *Lathrop 5894* (39); *Laughlin 1271* (6); *Leavenworth 795* (6), *886A* (6), *1336* (6); *Ledda 2988* (38); *Legname 499* (38), *5937* (38); *Leiboff 8* (38); *León 934* (6), *4099* (38), *4569* (12); *Leonard 7855* (12); *Leprieur 91* (23), *s.n.* (12), *s.n.* (29); *Lewis 720* (38), *801* (38); *Liesner 2120* (12), *4364* (6), *8453* (6), *10405* (23), *15783* (28), *15819* (28), *17160*/*** (35), *17630* (28), *19141* (28), *21308* (12), *22186*/*** (5), *22336* (28), *23630* (28), *23790** (28), *24975* (28); *Linares 1805* (29); *Liogier 15864* (13), *15976*** (13); *Lizama 1280* (39), *1308* (6); *Löfgreen 3841* (9); *López 28* (6), *93* (6); *Loen 132* (38); *Lot 1929* (6); *Luces 9* (38), *17* (38); *Luna 619* (38); *Lundell 951* (6), *1552* (6), *6427* (6), *14704*** (21), *16183* (6), *16206* (6); *Lyonnet 2663* (6).

MacDougal 3682 (20), *4177* (12); *Macedo 3008* (29); *Macías 3527* (6); *Madrid 125* (6), *589* (6); *Maguire 23456*/*** (31), *33197* (37), *54234* (3), *60323* (28); *Maldonado 1047* (38); *Marin 1241* (20); *Marinho 324* (12); *Martínez 130* (6), *183* (6), *2483* (6), *7075* (23), *12594*** (2), *14472* (12), *25239* (15), *27936* (6), *27938* (6), *29362* (6); *Mattos 12444* (23); *Matuda s.n.* (6); *McDaniel 13720* (12), *16819* (12); *McKee 11246* (37), *11291* (23); *McSaniel 24889* (12); *McVaugh 820* (6), *19109* (18), *20246*** (18); *Medina 32* (23), *121* (6); *Medrano F–1482* (6); *Mejía 9* (38); *Méndez 39* (29); *Meyer 796* (38), *3481* (38), *3754* (38); *Millán 415* (38); *Miranda 1057* (6); *Molina 30642* (6); *Montes 1341A* (9), *1661* (29), *3032* (9); *Moore 3487* (39); *Moreno 22115* (6), *24354* (6); *Mori 2127* (12); *Moritz 650* (29); *Morrone 462* (15), *524* (15), *566* (15), *2781* (38), *3095* (38), *3591* (38), *4669* (15), *4694* (14), *4702* (7), *4715* (20), *4721* (29), *4732* (20), *4734* (20), *4738* (20), *4740* (14), *4758* (15), *4769* (15), *4773* (14), *4776* (16), *4778* (29), *4780* (3), *4782* (3), *4783* (28), *4787* (14), *4788* (37), *4793* (29), *4797* (29), *4798* (3); *Morton 2559* (2), *6007* (23); *Mosier 250* (21); *Musch 1017* (38).

Nee 3643 (12), *7875* (12), *8185* (7), *10163* (29), *27682* (6), *27813* (12), *42747* (12), *42829* (12); *Nelson 4703* (29), *5039* (37), *7949* (12), *8621** (22); *Nicora 1857* (38), *6563* (38), *9019* (38), *17546* (38), *18526* (38); *Noblick 3063* (29); *Nolazco 1105* (6); *Novara 8790* (38); *Núñez 8927* (20).

Ortega 4102 (6); *Ortíz 878* (6), *1078* (12).

Palacios 136 (12); *Panero 5196* (18); *Parodi 10059* (20); *Partch 69–133* (29); *Pascual 471* (6); *Paz 30* (38); *Pedersen 8286* (38); *Pennell 7273* (20), *8164* (29); *Pensiero 111* (38), *3206* (38), *4457* (38); *Peterson 7199* (12), *9386* (20); *Philcox 3085* (9); *Pires 321* (12), *681* (12), *2722* (38), *2907* (29); *Pittier 535* (12), *538* (12), *659* (29), *1539* (29), *4719* (23), *6101* (12), *7235* (38), *9055* (29), *9517** (30), *10928* (12), *13438* (38), *13547* (38), *13668* (38); *Plowman 8772* (12), *9098* (9), *9411* (12); *Pohl 10015* (12), *10032* (12), *10050* (23), *10050* (29), *10051* (23), *10075* (29), *10313* (12), *10546* (6), *10978* (14), *11060* (29), *11378* (7), *11407* (23), *11566* (6), *11896* (29), *11921* (29), *12080* (12), *12287* (29), *12443* (29), *12586* (2), *12644* (6), *12694* (12), *12762* (29), *13058* (12), *13076* (6), *13146* (12), *13642* (2), *13819* (12), *15445* (29), *15555* (12), *112085* (6); *Poiteau s.n.* (23); *Prance 2861* (12), *9901* (9), *11923* (12), *11963* (13); *Pringle 3779* (6), *3991* (6); *Proctor 17961* (23); *Purpus 5026* (2), *8026** (2).

Quarín 104 (38); *Quintana 23 (6).*

Ramírez 605 (38), *1804* (12), *5583* (37); *Ramos 31* (9); *Reeder 1933* (6), *1972* (6), *2414* (18), *3007* (6), *4272* (6), *4301* (6), *4434* (6), *6126* (6); *Reis 79* (23); *Renvoize 3955* (12), *4055* (38), *4244* (12), *4625* (20); *Revilla 3094* (12); *Reyes 24* (6), *2575* (12); *Riggins 678* (15); *Rimachi 4428* (12), *7331* (12), *7748* (12); *Rivera 1788* (18); *Rodriguez 258* (38), *1561* (29), *3130* (12); *Roe 1787* (29); *Rohweder 2075* (6), *2169* (2); *Rojas 2313* (38), *2743* (38), *5474* (38), *6767* (9); *Rondon s.n.* (15); *Rose 9383* (6); *Rosengurtt B–3253* (38), *Rosengurtt 3399* (12), *Rosengurtt 5824* (38); *Rua 247* (29); *Rubio 140* (38); *Rudolph 83** (21); *Rúgolo 1725* (29), *1936* (29); *Runyon 4081* (6); *Rusby 23* (20), *248* (23); *Russell 1145* (37); *Rzedowski 17858* (18).

Salguero 4 (2); *Sandoval 392* (6); *Sandwith 1381*/*** (3); *Santana 883* (6), *2618** (18), *2970* (6), *3077* (6), *3728* (6), *3808* (18), *3811* (6); *Saravia Toledo 1224* (38), *10457* (38), *10536* (38), *12427* (38); *Saynes 2274* (6); *Schiefer 763* (23); *Schultes 17408* (12); *Schulz 3107* (38), *4145* (38), *10581*/*** (17), *10617* (17), *18072* (38); *Schunke 1505* (12); *Seidel 2861* (12), *3596* (12); *Sellow 1241* (36); *Sendulsky 607* (23); *Sergius 2682* (38); *Seymour 3436* (6), *3846* (6), *5137* (2), *5802* (29), *5803*** (22); *Silva 92*/*** (4); *Smith 176* (7), *2156* (23), *2157* (12), *2410* (37), *3412* (12), *6006* (12), *6582* (21), *6686* (12), *8339* (12), *9659* (20); *Sneider 4973* (12); *Soderstrom 464* (39), *980* (29), *981*/*** (37), *997* (37), *1158* (29); *Sohns 691* (6), *893* (29), *1376* (6), *1992* (6); *Solís 20533* (20); *Solomon 7549* (12), *8491a* (20), *12932* (20), *13003* (12), *13861* (20), *14950* (20), *17603* (20), *18908* (20), *18909* (12), *19036* (20); *Spellenberg 12207* (6); *Sperling 5583*/*** (8); *Spruce 22* (29), *25* (12); *Standley 12031* (6), *23596* (2), *23785* (6), *23905* (12), *25205* (29), *56363* (7), *56737* (6), *88678* (2); *Stanford 2269* (6), *2315* (38); *Stannard 17*** (12); *Stern 1187* (29), *1758* (12); *Stevens 3294* (6), *8189* (37), *8589* (37), *11806* (2), *14152* (12), *18098* (6), *20768* (23), *21736* (37), *25782* (6); *Steyermark 103* (28), *59455*** (28), *60501* (28), *74799* (28), *76010* (28), *87925* (3), *88630* (23), *96247* (12), *99281* (6), *117537* (28), *119537* (12), *122592* (6), *129723* (28), *130484* (28); *Sturkert 367** (38), *11716* (38), *12865* (38), *14048* (38); *Suarez 82* (6); *Swallen 2596* (6), *3666* (9), *3694* (9), *3873* (15), *4061* (9), *4069* (9), *4071* (9), *5017** (23), *5040* (12), *9432* (15), *10769* (6), *10778* (29), *10876* (6), *11002* (2), *11004* (2), *11027* (6), *11102* (29), *11151* (2), *11157* (6), *11243* (6), *11291* (6); *Sydow 6* (6); *Sytsma 2410* (12), *3941* (23).

Tamayo 3620 (12); *Tellez 8394* (29); *Tharp 43157* (6), *s.n.* (6); *Thomas 3454* (35); *Torres 743* (6), *982* (6); *Trejos 45102* (29); *Troncoso 3290* (38); *Trujillo 3593* (3); *Tsugara 461* (12); *Tuerckheim II–1452* (12); *Tyson 1366* (12), *2849* (12).

Ule 8031 (36); *Ulibarri 1649* (38); *Usteri 53* (9).

Valls 1055 (29), *1218* (29), *1219* (29); *Vara 376* (6); *Vásquez 10258* (12); *Vazquez Yanes 650* (6); *Venturi 645* (38), *732* (38), *2313* (38), *2322* (38), *2395* (38), *2533* (38), *5717* (38), *5718* (38), *7194* (38), *s.n.* (38); *Vera Santos 2300* (6), *2474* (6); *Vibrans 5427* (18), *5437* (6); *Vincent 6184* (29); *von Sneidern 159*** (20), *1283* (20); *von Tuerckheim 11452* (12).

Warming s.n. (36); *Weatherwax 218* (2); *Werff 7773* (15); *Williams 15727* (23); *Wingfield 5669* (6), *6485* (23), *6490* (6); *Wood 10200* (20); *Wooton s.n.* (6); *Woronow 7408* (30); *Wurdack 34325* (12), *39984* (34).

Yanez 791 (6).

Zardini 44193 (9); *Zarucchi 5345* (20), *6134* (20); *Zelaya 2304* (6); *Zucol 582* (38), *585* (38), *586* (38); *Zuloaga 3010* (38), *3621*** (38), *3871* (12), *3872* (12), *3942* (7), *3991* (15), *4188* (7), *4190** (29), *4260* (20), *4395* (14), *4414* (15), *4422* (37), *4441* (29), *4593* (29), *4608* (12), *4689* (29), *4725* (29), *4793* (15), *5839* (38), *6273* (38), *6959* (29), *7275* (15), *7305* (9), *7397* (39), *s.n.* (12).

sin colector 196 (6), *202* (39), *221* (6), *262* (6), *268* (6), *4375* (29).

Apéndice 3. Índice de Nombres Científicos.

Los sinónimos se indican en itálica.

Anachyris
Anachyris, subgénero
A. paspaloides
Brachiaria glabrinodis
B. grossaria
Ceresia
Ceresia, subgénero
C. elegans
C. aristata
Decumbentes, grupo
Dimorphostachys
D. adoperiens
D. botterii
D. ciliifera
D. drummondii
D. ghiesbreghtii
D. langei
D. monostachya
D. paspaloides
D. pedunculata
D. pilosa
D. schaffnerii
D. schaffnerii var. *remotispicula*
D. variabilis
Harpostachys, sección
Harpostachys, subgénero
Paniceae, tribu
Panicoideae, subfamilia
Panicum
P. campylostachyum
P. cinerascens
P. cultratum
P. decumbens
P. glabrinode
P. monobotrys
P. monostachyum
P. petrosum var. *mollis*
P. schaffneri
P. schumannii
P. squamatum
P. subfalcatum
P. thrasya
P. thrasyoides
P. unispicatum
Paspalum
Paspalum, subgénero
P. abbreviatum
P. achlysophilum
P. adoperiens
P. altsonii
P. auricomum
P. axillare
P. boivinii
P. botterii
P. campylostachyum
P. candidum
P. carajasense
P. ceresia
P. ciliiferum
P. cinerascens
P. crucense
P. culiacanum
P. cultratum
P. curvistachyum
P. decumbens
P. dimidiatum
P. dispar
P. dispar var. *marahuacense*
P. dissectum
P. drummondii
P. calliferum
P. foliiforme
P. glabrinode
P. glaziovii
P. graniticum
P. guatemalense
P. heteropodium
P. hintonii
P. hitchcockii
P. huberi
P. inconstans
P. lepidum
P. lineare
P. lloydii
P. longiligulatum
P. lucidulum
P. macrophyllum var. *piliferum*
P. malacophyllum
P. monostachyum
P. mosquitiense
P. multinervium
P. nutans
P. oreophilum
P. orinocense
P. palmeri
P. parvulum
P. paspaloides
P. peckii
P. pedunculatum
P. peregrinum
P. petilum
P. petrosum
P. pilosum
P. procerum
P. protensum
P. racemosum
P. ramianum
P. rectum var. *longispicatum*
P. reticulatum
P. robustum
P. scandens
P. schaffneri
P. schumannii
P. seminudum
P. setaceum var. *pubiflorum*
P. setosum
P. singulare
P. strictum
P. subfalcatum
P. thrasyoides

P. trinitense
P. unispicatum
P. vaginiflorum
P. variabile
P. varians
P. venezuelanum
Paspalanthium
Paspalanthium stoloniferum
Reimaria
R. candida
Thrasya
Thrasya, sección
Thrasya, subgénero
T. achlysophila
T. auricoma
T. axillaris
T. campylostachya
T. ciliatifolia
T. cinerascens
T. crucensis
T. cultrata
T. glaziovii
T. gracilis
T. granitica
T. guianensis
T. hirsuta
T. hitchcockii
T. longiligulata
T. mosquitiensis
T. oreophila
T. parvula
T. paspaloides
T. petrosa
T. petrosa var. *ciliata*
T. reticulata
T. robusta
T. scandens
T. schumannii
T. seminuda
T. setosa
T. stricta
T. thrasyoides
T. trinitensis
T. venezuelana
T. villosa
Tylothrasya
Tylothrasya petrosa

A REVISION OF *TRISETUM* (POACEAE: POOIDEAE: AVENINAE) IN SOUTH AMERICA[1]

Víctor L. Finot,[2] Paul M. Peterson,[3] Fernando O. Zuloaga,[4] Robert J. Soreng,[3] and Oscar Matthei[2]

ABSTRACT

A taxonomic treatment of *Trisetum* Pers. for South America, is given. Eighteen species and six varieties of *Trisetum* are recognized in South America. Chile (14 species, 3 varieties) and Argentina (12 species, 5 varieties) have the greatest number of taxa in the genus. Two varieties, *T. barbinode* var. *sclerophyllum* and *T. longiglume* var. *glabratum*, are endemic to Argentina, whereas *T. mattheii* and *T. nancaguense* are known only from Chile. *Trisetum andinum* is endemic to Ecuador, *T. macbridei* is endemic to Peru, and *T. foliosum* is endemic to Venezuela. A total of four species are found in Ecuador and Peru, and there are two species in Venezuela and Colombia. The following new species are described and illustrated: *Trisetum mattheii* Finot and *T. nancaguense* Finot, from Chile, and *T. pyramidatum* Louis-Marie ex Finot, from Chile and Argentina. The following two new combinations are made: *T. barbinode* var. *sclerophyllum* (Hack. ex Stuck.) Finot and *T. spicatum* var. *cumingii* (Nees ex Steud.) Finot. A key for distinguishing the species and varieties of *Trisetum* in South America is given. The names *Koeleria cumingii* Nees ex Steud., *Trisetum* sect. *Anaulacoa* Louis-Marie, *Trisetum* sect. *Aulacoa* Louis-Marie, *Trisetum* subg. *Heterolytrum* Louis-Marie, *Trisetum* subg. *Isolytrum* Louis-Marie, *Trisetum* subsect. *Koeleriformia* Louis-Marie, *Trisetum* subsect. *Sphenopholidea* Louis-Marie, *Trisetum malacophyllum* Steud., *Trisetum variabile* E. Desv., and *Trisetum variabile* var. *virescens* E. Desv. are lectotypified.

Key words: Aveninae, Gramineae, Poaceae, Pooideae, *Trisetum*.

RESUMEN

Se realizó un estudio taxonómico del género *Trisetum* en América del Sur. Se reconoció 18 especies y 6 variedades sudamericanas de *Trisetum*. Chile (14 especies, 3 variedades) y Argentina (12 especies, 5 variedades) poseen el mayor número de taxones del género *Trisetum*. Dos variedades, *T. barbinode* var. *sclerophyllum* y *T. longiglume* var. *glabratum*, son endémicos de Argentina, mientras *T. mattheii* y *T. nancaguense* se conocen sólo para Chile. Cuatro especies se encuentran en Ecuador y Perú y dos especies en Venezuela y Colombia. *Trisetum andinum* es endémica del Ecuador, *T. macbridei* es endémica del Perú, y *T. foliosum* es endémica de Venezuela. Se describen e ilustran las siguientes nuevas especies: *Trisetum mattheii* Finot y *T. nancaguense* Finot, de Chile, y *T. pyramidatum* Louis-Marie ex Finot, de Chile y Argentina. Se establecen las siguientes dos nuevas combinaciones: *T. barbinode* var. *sclerophyllum* (Hack. ex Stuck.) Finot y *T. spicatum* var. *cumingii* (Nees ex Steud.) Finot. Se entrega una clave para separar las especies y variedades de *Trisetum* en Sudamérica. Los nombres *Koeleria cumingii* Nees ex Steud., *Trisetum* sect. *Anaulacoa* Louis-Marie, *Trisetum* sect. *Aulacoa* Louis-Marie, *Trisetum* subg. *Heterolytrum* Louis-Marie, *Trisetum* subg. *Isolytrum* Louis-Marie, *Trisetum* subsect. *Koeleriformia* Louis-Marie, *Trisetum* subsect. *Sphenopholidea* Louis-Marie, *Trisetum malacophyllum* Steud., *Trisetum variabile* E. Desv., y *Trisetum variabile* var. *virescens* E. Desv. fueron lectotipificados.

The genus *Trisetum* was described by Persoon (1805), including 11 species previously treated under *Avena* L. As currently defined, *Trisetum* comprises about 70 species of perennial grasses, inhabiting temperate and cold zones in both hemispheres (Louis Marie, 1928, 1929; Swallen, 1948; Tsvelev, 1970, 1983; Jonsell, 1980; Veldkamp & Van der Have, 1983; Clayton & Renvoize,

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[2] Universidad de Concepción, Facultad de Agronomía, Casilla 537, Chillán, Chile. vifinot@udec.cl.

[3] Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, DC 20013-7012, U.S.A. peterson@si.edu; sorengr@si.edu.

[4] Instituto de Botánica Darwinion, Labardén 200, San Isidro, Argentina. fzuloaga@darwin.edu.ar.

1986; Pohl & Davidse, 1994; Tucker 1996; Edgar, 1998; Finot et al., 2004). In America, the genus is distributed from Greenland to southern South America, ranging from approximately 69°N to 55°S (Hultén, 1959; Nicora, 1978).

Trisetum has been traditionally divided in two sections: section *Trisetum*, typified by *T. flavescens* (L.) P. Beauv., with lax, open panicles and culms glabrous below the inflorescence, and section *Trisetaera* Asch. & Graebn., typified by *T. spicatum* (L.) K. Richt., with dense, spiciform panicles and culms pilose below the inflorescence. This supraspecific classification has been accepted by most authors (Chrtek, 1965; Chrtek & Jirásek, 1963; Tsvelev, 1983). Chrtek (1965) divided *Trisetum* in four subgenera: subgenus *Trisetum*, subgenus *Distichotrisetum* Chrtek, subgenus *Glaciotrisetum* Chrtek, and subgenus *Graciliotrisetum* Chrtek and divided subgenus *Trisetum* into five sections: section *Trisetum*, section *Trisetaera* Asch. & Graebn., section *Rigida* Chrtek, section *Hispanica* Chrtek, and section *Carpatica* Chrtek. Only the *Trisetum* sections *Trisetum* and *Trisetaera* include American representatives.

A general account of the American taxa was first made by Steudel (1853–1855), who described ten species for South America: *Trisetum andinum* Benth., *T. barbatum* Steud., *T. hirtum* Trin., *T. caudulatum* Trin., *T. barbinode* Trin., *T. splendidulum* Steud., *T. airiforme* Steud., *T. heteronymum* Steud., *T. malacophyllum* Steud., and *T. phleoides* (d'Urv.) Kunth. Hitchcock (1927) later recognized the following six species from Ecuador, Peru, and Bolivia: *Trisetum deyeuxioides* (Kunth) Kunth, *T. scabrifolium* Hitchc., *T. floribundum* Pilg., *T. macbridei* Hitchc., *T. spicatum* (L.) K. Richt., and *T. andinum* Benth.

Louis-Marie (1928, 1929), in his taxonomic revision of *Trisetum*, recognized 60 species for America. However, Louis-Marie had a very broad concept of *Trisetum* that included several species later transferred to other genera, including *Bromus*, *Deschampsia*, *Dielsiochloa*, *Graphephorum*, *Leptophyllochloa*, *Peyritschia*, and *Sphenopholis* (Valencia, 1941; Pilger, 1943; Parodi, 1949a; Erdman, 1965; Nicora, 1978; Finot, 2003; Finot et al., 2004). Louis-Marie (1928, 1929) divided the genus *Trisetum* into two subgenera (Table 1; see Appendix 3 for subgeneric lectotypifications): subgenus *Heterolytrum* Louis-Marie and subgenus *Isolytrum* Louis-Marie. He divided *Trisetum* subg. *Heterolytrum* into two sections: section *Anaulacoa* Louis-Marie (including subsect. *Trisetum*, subsect. *Sphenopholidea* Louis-Marie, subsect. *Graphephorum* (Desv.) Louis-Marie, subsect. *Koeleriformia* Louis-Marie, and subsect. *Deschampsioidea* Louis-Marie) and section *Aulacoa* Louis-Marie. South American species in *Trisetum* sect. *Anaulacoa* subsect. *Trisetum* included: *T. splendidulum*, *T. irazuense* (Kuntze) Hitchc., *T. fraudulentum* Steud., *T. malacophyllum* Steud., *T. cernuum* Trin., *T. heteronymum* Steud., *T. hirtum* Trin., *T. mollifolium* Louis-Marie, *T. oreophilum* Louis-Marie var. *oreophilum*, *T. oreophilum* var. *johnstonii* Louis-Marie, *T. lasiolepis* E. Desv., *T. preslei* (Kunth) E. Desv., *T. spicatum* var. *spicatum*, *T. spicatum* var. *hirsutum* Louis-Marie, *T. spicatum* var. *phleoides* (Kunth) Macloskie, *T. spicatum* var. *fuegianum* (Hack.) Louis-Marie, *T. spicatum* var. *dianthemum* Louis-Marie, *T. spicatum* var. *andinum* (Benth.) Louis-Marie, *T. barbinode* Trin. var. *barbinode*, *T. barbinode* var. *hirtiflorum* (Hack.) Louis-Marie, *T. caudulatum* Trin., *T. variabile* E. Desv. var. *variabile*, *T. variabile* var. *flavescens* E. Desv., *T. variabile* var. *virescens* E. Desv., *T. variabile* var. *chiloense* (Phil.) Louis-Marie, *T. variabile* var. *vidalii* (Phil.) Louis-Marie, *T. erectum* Phil., *T. monticola* Phil., and *T. paradoxum* Phil. In *Trisetum* subsect. *Koeleriformia* Louis-Marie included the following seven species: *T. laxiflorum* Phil., *T. araeanthum* Phil., *T. brachyatherum* Phil., *T. depauperatum* Phil., *T. micratherum* E. Desv., *T. nemorosum* Phil., and *T. laxum* Phil. *Trisetum micratherum* was later transferred to *Leptophyllochloa* by Calderón (1978) (*L. micrathera* (E. Desv.) C. E. Calderón). *Trisetum* subsect. *Sphenopholidea* and subsection *Graphephorum* do not have South American representatives. Louis-Marie included two South American species: *T. brasiliense* Louis-Marie and *T. juergensii* Hack., in *Trisetum* subsect. *Deschampsioideum*. In *Trisetum* sect. *Aulacoa* Louis-Marie included two species, *Bromus trinii* E. Desv. (replaced name *Trisetum hirtum* Trin. = *Bromus berteroanus* Colla) and *T. floribundum* Pilg. (= *Dielsiochloa floribunda* (Pilg.) Pilg.). South American representatives of *Trisetum* subg. *Isolytrum* included *T. deyeuxioides*, *T. longiglume* Hack., *T. andicola* Louis-Marie, *T. evolutum* (E. Fourn.) Hitchc., and *T. macbridei* Hitchc.

Valencia (1941) placed *Trisetum juergensii*, *T. confertum* Pilg., *T. brasiliense*, and *T. andicola* in *Deschampsia*. However, Parodi (1949b) disagreed with Valencia concerning the position of *T. andicola*. According to Parodi (1949b), a lemma with two apical setae produced by the apical extension of the intermediate nerves supports the recognition of this species in genus *Trisetum*.

Hultén (1959) reviewed the taxonomy of the *Trisetum spicatum* complex on a world-wide basis and he cited several South American taxa, including a new subspecies, *T. spicatum* subsp. *bolivianum*

Hultén from La Paz, Bolivia. Hultén did not treat most of the varieties of *T. spicatum* s.l. mentioned by Louis-Marie for South America.

In addition to the European *T. flavescens* introduced in North and South America, Nicora (1978) recognized 13 species in Patagonia: *T. cernuum*, *T. longiglume* Hack., *T. tomentosum* (E. Desv.) Nicora, *T. spicatum*, *T. phleoides* (d'Urv.) Kunth, *T. cumingii* (Nees ex Steud.) Nicora, *T. lechleri* (Steud.) Nicora, *T. caudulatum*, *T. barbinode*, *T. hirtiflorum* Hack., *T. sclerophyllum* Hack., *T. lasiolepis* E. Desv., and *T. preslei* (Kunth) E. Desv. Later, Rúgolo de Agrasar and Nicora (1988) described a new species, *T. ambiguum* Rúgolo & Nicora, from Argentina.

Several species are controversial in the generic alignment. Although *Trisetum* subsect. *Deschampsioideum* is retained for several species of Mexico and Central America (Finot et al., 2004), *T. brasiliense* and *T. juergensii* of South America do not fit well in the genus and will be dealt with in future papers. In addition, we recognize *Trisetum confertum* as *Peyritschia conferta* (Pilg.) Finot (Finot, 2003).

Our current treatment of *Trisetum* for the Americas recognizes 45 species and 20 varieties (Finot, 2003; Finot et al., 2004; this paper). In this paper we recognize 18 species and six varieties for South America (see Appendix 1 for alphabetical list). We describe and illustrate three new species of *Trisetum* (*T. mattheii* Finot, *T. nancaguense* Finot, and *T. pyramidatum* Louis-Marie ex Finot), make two new combinations (*T. barbinode* var. *sclerophyllum* (Hack. ex Stuck.) Finot and *T. spicatum* var. *cumingii* (Nees ex Steud.) Finot), and provide descriptions and keys to the species and varieties in South America.

Material and Methods

Type specimens and general collections from the following herbaria were studied: BA, BAA, BAF, CONC, CTES, CR, F, LP, MERL, P, QCA, S, SI, US, and ZOELLNER. In some cases, the curators of these herbaria sent us digital photographs or Xerox copies of types, or we had access to internet digital images (C, PR, NY). Abbreviations for herbaria correspond to those cited by Holmgren et al. (1990), except ZOELLNER, which is the personal herbarium of Otto Zoellner, Quilpué, Chile. An index to specimens examined and a list of all names and synonyms mentioned in this manuscript, including those in the introduction, are treated in Appendix 2 and 4, respectively.

In the morphological descriptions the length given for florets was usually taken from the first or lowest floret. If there were three or more florets per spikelet, then the second floret was sometimes used to calculate the range. Therefore, when using our keys to determine South American specimens of *Trisetum* it is best to measure only the first or lowest floret.

Key to *Trisetum* and Morphologically Similar Genera in South America

1a. Plants annual.
  2a. Plants 20–250 cm tall; panicles lax, open; spikelets 15–50 mm long, pendulous; glumes equal in length; lemmas dorsally awned, the awn geniculate and bent at the base; ovary pilose; caryopsis with solid endosperm ..... *Avena*
  2b. Plants 3–50 cm tall; panicles dense, spiciform; spikelets 2.8–4.5(–7) mm long; glumes unequal in length; lemmas muticous or with a short subapical awn up to 3 mm long; ovary glabrous; caryopsis with liquid endosperm ..... *Rostraria*
1b. Plants perennial, caespitose, rhizomatous or with bulbous bases.
  3a. Spikelets 7- to 9-flowered, with 2 or 3 fertile basal florets and 4 to 6 sterile upper florets; rachilla disarticulating only immediately above the glumes, florets falling as a collective unit ..... *Dielsiochloa*
  3b. Spikelets (1)2- to many-flowered, without sterile florets or the terminal floret reduced; rachilla disarticulating above the glumes and between the florets (except *Arrhenatherum* where 2 florets fall together).
    4a. Lemmas muticous or with a small awn inserted near the apex, the awn straight.
      5a. Panicles lax, open; lemmas 3-nerved ..... *Leptophyllochloa*
      5b. Panicles contracted, subspiciform; lemmas 5-nerved.
        6a. Lemmas strongly scabrous, the keel with shining ciliate hairs; florets with a single stamen ..... *Raimundochloa*
        6b. Lemmas glabrous, the keel scabrous, rarely ciliate (ciliate in *Koeleria fueguina* C. E. Calderón ex Nicora); florets with 3 stamens.
          7a. Spikelets 2- or 3(4)-flowered; ovary glabrous or with a few short hairs near the apex; caryopsis fusiform, without a ventral groove, hilum punctiform, endosperm liquid ..... *Koeleria*
          7b. Spikelets (1)2(3)-flowered; ovary pilose; caryopsis sub-triangular, with a ventral groove, hilum linear, 1/5–1/3 as long as the caryopsis; endosperm solid ... *Relchela*
    4b. Lemma with a dorsal awn inserted well below the apex, the awn geniculate and bent.
      8a. Spikelets 2-flowered; the lower floret staminate with a large geniculate awn inserted on the

Table 1. Infrageneric classification of the South American species of *Trisetum* in Louis-Marie's (1928, 1929) and our taxonomic treatment. Accepted taxa are presented in **bold**.

Louis-Marie (1928, 1929)	This treatment
Genus **Trisetum**	Genus **Trisetum**
	Subg. *Trisetum*
	(Subg. **Trisetum**)
	(Subg. **Trisetum** sect. **Trisetum**)
Subg. *Heterolytrum*	
Sect. *Anaulacoa*	
Subsect. *Trisetum* (as *Eutriseta*)	Sect. **Trisetum**
T. cernuum Trin., *T. fraudulentum* Steud.	**T. cernuum**
T. irazuense (Kuntze) Hitchc.	**T. irazuense**
T. flavescens (L.) P. Beauv.	**T. flavescens**
	T. foliosum Swallen
	Sect. **Trisaetera** Asch. & Graebn.
T. spicatum var. *andinum* (Benth.) Louis-Marie	**T. ambiguum** Rúgolo & Nicora
	T. andinum Benth.
T. barbinode Trin. var. **barbinode**	**T. barbinode** var. **barbinode**
T. barbinode var. **hirtiflorum** (Hack.) Louis-Marie	**T. barbinode** var. **hirtiflorum**
	T. barbinode var. **sclerophyllum** (Hack.) Finot
T. caudulatum Trin., *T. splendidulum* Steud., *T. heteronymum* Steud., *T. variabile* var. *flavescens* E. Desv., *T. variabile* var. *virescens* E. Desv., *T. variabile* var. *chiloense* (Phil.) Louis-Marie, *T. variabile* var. *vidalii* (Phil.) Louis-Marie, *T. monticola* Phil.	**T. caudulatum** Trin. var. **caudulatum**
	T. caudulatum Trin. var. **correae** Nicora
T. spicatum var. *dianthemum* Louis-Marie	**T. dianthemum** (Louis-Marie) Finot
	T. longiglume Hack.
	T. longiglume var. **glabratum** Nicora
	T. macbridei Hitchc.
	T. mattheii Finot
	T. naneaguense Finot
T. oreophilum var. **johnstonii** Louis-Marie	**T. oreophilum** var. **johnstonii**
T. oreophilum Louis-Marie var. **oreophilum**	**T. oreophilum** var. **oreophilum**
T. spicatum var. *hirsutum* Louis-Marie, *T. spicatum* var. *phleoides* (d'Urv.) Macloskie	**T. phleoides** (d'Urv.) Kunth
T. preslei (Kunth) E. Desv., *T. lasiolepis* E. Desv.	**T. preslei**
	T. pyramidatum Louis-Marie ex Finot
T. spicatum (L.) K. Richt., *T. spicatum* var. *fuegianum* (Hack.) Louis-Marie	**T. spicatum**
T. malacophyllum Steud., *T. mollifolium Louis-Marie*	
T. hirtum Trin.	
	T. spicatum var. **cumingii** (Nees ex Steud.) Finot
	Bromus sect. **Neobromus** (Shear) Hitchc.
	B. berteroanus Colla
Trisetum erectum Phil.	Unknown status
T. paradoxum Phil.	Unknown status
Subsect. *Koeleriformia*	**Leptophyllochloa** C. E. Calderón
T. laxiflorum Phil., *T. araeanthum* Phil., *T. brachyatherum* Phil., *T. depauperatum* Phil., *T. nemorosum* Phil., *T. laxum* Phil.	**L. micranthera** (E. Desv.) C. E. Calderón

Table 1. Continued.

Louis-Marie (1928, 1929)	This treatment
Subsect. *Deschampsioidea* Louis-Marie	Subg. **Deschampsioideum** (Louis-Marie) Finot (without representatives in South America)
Trisetum brasiliense Louis-Marie	**Deschampsia brasiliensis** (Louis-Marie) Valencia
Subsect. *Sphenopholidea* Louis-Marie (without representatives in South America)	**Sphenopholis** Scribn. (without representatives in South America)
Subsect. *Graphephorum* (Desv.) Louis-Marie (without representatives in South America)	**Graphephorum** Desv. (without representatives in South America)
Sect. *Aulacoa*	**Dielsiochloa** Pilg.
T. trinii (E. Desv.) Louis-Marie	**Bromus berteroanus** Colla
T. floribundum Pilg.	**Dielsiochloa floribunda** (Pilg.) Pilg.
Subg. *Isolytrum*	
T. deyeuxioides (Kunth) Kunth, *T. evolutum* (E. Fourn.) Hitchc.	**Peyritschia deyeuxioides** (Kunth) Finot
T. longiglume Hack., *T. andicola* Louis-Marie	see **T.** sect. **Trisaetera**
T. macbridei Hitchc.	see **T.** sect. **Trisaetera**

lower 1/3 of the lemma; upper floret perfect, the apex muticous or with a small subapical awn ..... *Arrhenatherum*

8b. Spikelets (1)2- to many-flowered; florets all perfect.

9a. Spikelets 3- to 8-flowered; lemmas 7- to 9-nerved; panicles terminal and with cleistogamous axillary panicles ..... *Amphibromus*

9b. Spikelets (1)2- or 3(to 6)-flowered; lemmas 5-nerved; panicles terminal and, if present, axillary panicles not cleistogamous.

10a. Culms with a bulbous base; panicles spiciform; glumes shorter than all florets (together); lemmas rounded on the back, the awn inserted near the middle; lemma apex bilobed, hyaline; callus acute ..... *Helictotrichon*

10b. Culms without a bulbous base; panicles open or spiciform; glumes shorter to longer than all florets; lemma keeled, somewhat laterally flattened, the awn inserted on the upper 1/3; lemma apex bidentate with intermediate nerves prolonged into setae; callus obtuse ..... *Trisetum*

Taxonomic Treatment

Trisetum Pers., Syn. Pl. 1: 97. 1805. TYPE: *Trisetum flavescens* (L.) P. Beauv., Ess. Agrostogr. 88, 153, t. 18, f. 1. 1812, lectotype, designated by Hitchcock, U.S.D.A. Bull. 772: 107–109. 1920.

Rupestrina Prov., Fl. Canad.: 689. 1862. TYPE: *Rupestrina pubescens* Prov. (= *Trisetum spicatum* (L.) Richt.)

Perennials, caespitose, sometimes shortly rhizomatous; culms 5–300 cm tall, erect to geniculate at base, glabrous or pubescent. Leaf sheaths glabrous or pubescent, longer or shorter than the internodes; blades flat, conduplicate, convolute or involute, soft, rarely rigid; ligule membranous. Inflorescence in panicles contracted or open, spiciform, ovate or pyramidal; the rachis glabrous, scabrous, or pubescent. Spikelets (1)2- to 6-flowered, short pedicellate; rachilla pubescent or glabrous, usually prolonged beyond the upper floret; disarticulation above the glumes and between the florets; glumes heteromorphic, lanceolate to ovate-lanceolate, equal or unequal, first glume 1- to 3-veined, usually shorter and narrower than the second, second glume 3- to 5-nerved; lemmas lanceolate, (3 to)5(to 7)-veined, usually awned or muticous, with apex and margins hyaline, glabrous or pubescent, slightly keeled and compressed, rarely terete; apex with 2 to 4 short awns, entire, or 2-toothed; central awn from the upper 1/3, rarely the middle, of the subapical portion of the lemma; awn exerted, geniculate or merely divaricate; callus short pilose; palea not tightly enclosed by the margins of the lemma (gaping), 2-keeled, hyaline, usually shorter than the lemma; stamens 3, anthers 0.3–4.5 mm long; lodicules 2, membranous; ovary glabrous or with short and shining trichomes near the apex. Caryopses compressed, soft; hilum short, punctiform; endosperm solid or liquid, soft or hard. Basic chromosome number $x = 7$.

Comments. Our subgeneric treatment of the

species that occur in South America includes a single subgenus: *Trisetum* subg. *Trisetum* with two sections: section *Trisetum* and section *Trisetaera*. In the following key we have indicated in which section each species resides (see leads 1a and 1b). Species numbered 1–4 are placed in *Trisetum* sect. *Trisetum* and species numbered 5–18 are placed in *Trisetum* sect. *Trisetaera*. A description of *Trisetum* subg. *Trisetum* and *Trisetum* sects. *Trisetum* and *Trisetaera* appears in Finot et al. (2004).

Key to Species and Varieties of *Trisetum* in South America

1a. Panicles lax, mostly open or narrow, pyramidal, never spiciform; culms glabrous below the inflorescence; glumes unequal, the first glume shorter and narrower than the second glume; glumes notably shorter than the florets (*Trisetum* sect. *Trisetum*).
2a. Sheath apex notably extended upward on one side as an appendix as long as the ligule ... 3. *T. foliosum*
2b. Sheath apex not extended as an appendix.
3a. Ovary and caryopsis hairy at the apex; panicles few-flowered, the lower branches usually naked below; first glume 0.5–5 mm long, sometimes reduced; ligule 1.5–7 mm long ..... 1. *T. cernuum*
3b. Ovary and caryopsis glabrous at the apex; panicles densely-flowered, branches not naked below; first glume 2–5 mm long, never reduced.
4a. Panicles usually gold-yellowish; lemmas not strongly scabrous; ligule 0.5–2 mm long; leaf blades (3–)10–16 cm long, 2–4 mm wide ..... 2. *T. flavescens*
4b. Panicles greenish to purplish; lemmas strongly scabrous; ligule 2–4 mm long; leaf blades 20–30 cm long, 2.5–6 mm wide ..... 4. *T. irazuense*
1b. Panicles spiciform to contracted, never open; culms pubescent or hairy below the inflorescence, rarely glabrous to subglabrous; glumes subequal, a little shorter, equal or longer than the florets (*Trisetum* sect. *Trisetaera*).
5a. Lemma hairy, the hairs usually more than 0.5 mm long.
6a. Plants small, usually less than 20 cm tall; panicle dense, spiciform.
7a. Leaf glabrous; glumes equaling or slightly exceeding the florets; first glume 1.5–6 mm long; second glume (4.5–)5.5–6.6 mm long ..... 16. *T. preslei*
7b. Leaf hairy; glumes shorter than the florets; first glume 2.7–4 mm long; second glume 3.3–4.7 mm long ..... 14b. *T. oreophilum* var. *johnstonii*
6b. Plants taller, usually more than 30 cm tall; panicle spiciform or contracted.
8a. Glumes longer or equaling the florets, the second glume usually longer than the florets; first glume 1- or 3-nerved; leaf glabrous.
9a. Panicles contracted, pale green, up to 15 cm long; glumes unequal; second glume 6.5–10 mm long; leaf blades soft ..... 7a. *T. barbinode* var. *barbinode*
9b. Panicles spiciform, gold-purple, (2–)3–5(–8) cm long; glumes subequal to unequal; second glume 5–8 mm long.
10a. Ovary glabrous; blades stiff ..... 7c. *T. barbinode* var. *sclerophyllum*
10b. Ovary with short trichomes on the apex; blades soft ..... 7b. *T. barbinode* var. *hirtiflorum*
8b. Glumes shorter than the florets; first glume 1-nerved; leaf blades pubescent.
11a. Panicles silvery-green to weakly purple, not purplish; spikelets 5.5–8 mm long; first glume 3.5–6 mm long; second glume 5.3–7.6 mm long ..... 13. *T. nancaguense*
11b. Panicles green-purplish to strongly purplish; spikelets 3.5–5 mm long; first glume 2.2–4.5 mm long; second glume 2.8–4.7 mm long.
12a. Panicles 0.8–1.5 cm wide, dense, many-flowered; spikelets 3.5–4.5 mm long; first glume 2.2–3.6 mm long; second glume 2.8–4.1 mm long ..... 14a. *T. oreophilum* var. *oreophilum*
12b. Panicles 0.5–0.8 cm wide, narrow, few-flowered; spikelets 4.5–5 mm long; first glume 3.5–4.5 mm long; second glume 3.8–4.7 mm long ..... 12. *T. mattheii*
5b. Lemma glabrous or scabrous, never hairy, but rarely covered with very short hairs, the hairs shorter than 0.5 mm long.
13a. Panicles no more than 3 to 4 times as long as wide, dark purplish; plants velvety; lemma scabrous or covered with very short trichomes giving a velvety texture ..... 6. *T. andinum*
13b. Panicles more than 3 to 4 times as long as wide, green to more or less purplish; plants glabrous or pilose, not velvety; lemmas glabrous or scabrous, not velvety.
14a. Glumes longer than the florets, subequal in length and width.
15a. Plant totally pubescent; glumes ciliate on the keel; first glume 4–6.5 mm long, second glume 5–6.5 mm long ..... 15. *T. phleoides*
15b. Plants not totally pubescent; glumes scabrous on the keel, not ciliate; glumes more than 6–9.5 mm long.
16a. Glumes 7.5–8 mm long, ovate, exceeding the florets by 1/3–1/2 in length; blades pilose ..... 11. *T. macbridei*
16b. Glumes 6–9.5 mm long, lanceolate, exceeding the florets by 1/4–1/3 in length; blades glabrous.

17a. Spikelets 6.5–8 mm long; awn borne on the upper 1/3 of the lemma; callus trichomes short (ca. 0.2 mm long); ovary glabrous at the apex ..... 9. *T. dianthemum*

17b. Spikelets 9–10 mm long; awn borne on the middle of the lemma; callus trichomes long, reaching 1/2–3/4 the length of the lemma; ovary with or without trichomes at the apex.

18a. Panicles ovoid, dense, subspiciform, many-flowered; ovary and caryopsis with short, curved and shining trichomes near the apex; caryopsis 2–2.7 mm long; anthers (0.5–)0.8–1 mm long ..... 10a. *T. longiglume* var. *longiglume*

18b. Panicles linear, narrow, few-flowered; ovary and caryopsis glabrous near the apex; caryopsis 3.5–4.2 mm long; anthers 1.3–1.7 mm long ..... 10b. *T. longiglume* var. *glabratum*

14b. Glumes equal or shorter than the florets, dissimilar in length and width, or the first glume shorter and the second glume longer than the florets and first glume shorter and narrower than the second glume.

19a. Spikelets 1-flowered; ovary with a few trichomes at the apex; lemma conspicuously nerved toward the apex, the intermediate and marginal nerves prolonged beyond the apex as four short apical awns ..... 5. *T. ambiguum*

19b. Spikelets 2- or 3(to 5)-flowered; ovary glabrous at the apex; lemma inconspicuously nerved toward the apex, the intermediate nerves prolonged beyond the apex as 2 setae or short apical awns, the marginal nerves not prolonged beyond the apex.

20a. Second glume longer than the spikelet, the first glume shorter than the spikelet.

21a. Plants rhizomatous; panicle pyramidal, contracted, not spiciform, 7–11 cm long, 2–3 cm wide; paleas always shorter than the lemma ..... 17. *T. pyramidatum*

21b. Plants caespitose; panicle spiciform, dense, 4–10 cm long, 0.8–2 cm wide; paleas a little shorter than the lemma in the first floret and longer than the lemma in the upper floret ..... 18b. *T. spicatum* var. *cumingii*

20b. Glumes (second and first) shorter than the florets.

22a. Glumes similar in width, the first glume 0.5–1 mm wide, first glume as wide as second glume or a little narrower; culms densely pubescent below the panicles; blades glabrous or pilose; spikelets 2- or 3-flowered ..... 18a. *T. spicatum* var. *spicatum*

22b. Glumes dissimilar in width, the first glume 0.3–0.5 mm wide, narrower than the second glume; culm glabrous to subglabrous below the panicles; blades pilose; spikelets 2- to 4(5)-flowered.

23a. Ovary and caryopsis glabrous at the apex ..... 8a. *T. caudulatum* var. *caudulatum*

23b. Ovary and caryopsis with trichomes at the apex ..... 8b. *T. caudulatum* var. *correae*

Trisetum subg. **Trisetum** sect. **Trisetum**

1. Trisetum cernuum Trin., Mém. Acad. Imp. Sci. St. Pétersbourg Sér. 6, Sci. Math. 1 (1): 61. 1830. *Avena cernua* (Trin.) Kunth, Rev. Gen. 1, suppl. 26. 306. 1833. TYPE: U.S.A. Alaska, Sitka, *J. F. G. von Eschscholtz s.n.* (holotype, LE not seen; isotypes, BAA-3366!, P!, US-81779!).

Avena leptostachys Hook. f., Fl. Antarct.: 378. 1846. TYPE: Chile. Strait of Magalhaens, Port Famine, 1826, *Capt. King s.n.* (holotype, K not seen; isotypes, SGO ex K!, US-fragm. ex K!).

Trisetum fraudulentum Steud., Syn. Pl. Glumac. 1: 424. 1854. TYPE: Chile. Sandy Point, Magellan, *W. Lechler 1283* (holotype, P!; isotypes, CONC fragm. ex P!, US-868480 fragm. ex LE!, US fragm. ex P-STEUD-434 & photo!).

Perennial, with short rhizomes; culms 35–85 cm tall, glabrous, up to 3 mm diam. near base, somewhat geniculate; nodes 2 to 4, glabrous. Leaf sheaths longer or shorter than the internodes, glabrous or more rarely sparsely pilose; ligule 1.5–7 mm long, longer in the upper leaves, oval, fimbriate, ciliate on the margins, the dorsal surface glabrous or more frequently pilose; blades 10–22 × 0.3–1.2 cm, flat, soft, glabrous or sparsely pubescent adaxially. Panicles 6–30 × 2–5 cm, lax, open, nodding, green or purple; the branches capillary, flexuous, the lower branches usually naked toward the base or with spikelets to the base. Spikelets 4.5–12 × 2–4 mm, (2)3- or 4-flowered; pedicels 1–4.5 mm long, capillary, flexuous, glabrous or scabrous; rachilla 1.5–2 mm long, pilose with stiff trichomes 1–2 mm long; glumes shorter than the florets, 1/2 to 2/3 as long as the spikelet, very unequal to subequal in length and very unequal in width, the first glume narrower than the second; keel smooth to scaberulous; margins hyaline, sometimes scabrous-ciliate; first glume 0.5–5 × 0.1–0.5 mm, usually 1/2–2/3 as long as the second glume,

linear-lanceolate, attenuate, 1-nerved, sometimes reduced; second glume 3–7.5 × 0.5–1 mm, oval-lanceolate, 3-nerved; florets 5–8.5 × 0.7–1 mm; lemmas linear-lanceolate, glabrous, scabrous toward the apex, awned, green or tinged with purple on the margins and apex; apex 2-aristulate, the aristae 0.5–1.5 mm long; awn 6–16 mm long, borne on the upper 1/3 ca. 1.5–2.5 mm below the apex, curved, not strongly twisted nor geniculate, scabrous, up to 3 times as long as the lemma; callus obtuse, pubescent, the trichomes 0.2–0.7 mm long; paleas 3.5–5.7 mm long, shorter than the lemma, hyaline, 2-nerved, the nerves scabrous; apex bidentate; anthers 0.5–1.5 mm long; lodicules 0.7–0.8 mm long; apex bilobed; ovary with short and curved trichomes near the apex. Caryopses 2.5 × 1 mm, hairy at the apex; endosperm soft.

Distribution and habitat. Disjunct, occurring in western North America, west of the Rocky Mountains, from southwestern Alaska to northern California, and in southern South America. In South America, *Trisetum cernuum* occurs in Patagonia of Argentina and Chile usually below 2000 m, from 38°S to approximately 55°S, south of Estrecho de Magallanes. In Chile, it grows from the Region IX (Malleco, ca. 38°S) to the Region XII (Isla Navarino, ca. 54°55′S). In Argentina, *T. cernuum* is found in Chubut, Neuquén, Río Negro, and Tierra del Fuego (Nicora, 1978; Zuloaga et al., 1994), from 38°S in Chubut to 54°47′S in Ushuaia. This species is frequently associated with moist woods of *Araucaria araucana* (Mol.) K. Koch-*Nothofagus dombeyi* (Mirb.) Oerst. and *Nothofagus pumilio* (Poepp. & Endl.) Krasser, and "mallines" forests between sea level and 1500 m.

Phenology. Flowering between January and March.

Illustrations. Hitchcock and Chase (1950: 289, fig. 389); Nicora (1978: 242, fig. 156 A–D).

Comments. *Trisetum cernuum* is a well-defined species, easily recognized by its lax, open, nutant panicles with subverticillate and paucispiculate branches, the lower ones without spikelets below the middle, spikelets with dissimilar glumes, glumes shorter than the spikelets, and caryopses with short hairs at the apex. These hairs, very typical in the genus *Trisetum*, are also present in other South American species such as *T. ambiguum*, *T. caudulatum* var. *correae*, *T. barbinode* var. *hirtiflorum*, and *T. longiglume* var. *longiglume*. All these species are restricted to Chile and Argentina, and they are easily distinguished from *T. cernuum* by their spiciform panicles. *Trisetum cernuum* shows extreme variation in glume length, especially in the first glume. The first glume, usually 2–3.8 mm long, can be reduced to 0.5 mm long. However, we found spikelets with reduced and non reduced glumes in the same plants (e.g., *Bolander 6122*, collected in California, U.S.A.). *Trisetum cernuum* is morphologically similar to *T. flavescens* and *T. irazuense*. *Trisetum cernuum* differs from *T. flavescens* in having paucispiculate panicles, hairy caryopses, and shorter glumes that are sometimes reduced. *Trisetum flavescens* has multispiculate panicles, glumes that are never reduced, and caryopses that are glabrous at the apex. *Trisetum flavescens* is a European species, introduced in southern South America as a forage plant (Nicora, 1978). *Trisetum irazuense* differs from *T. cernuum* in having lemmas strongly scabrous and the ovary glabrous at the apex. It shares with *T. cernuum* lax, open panicles, spikelets with glumes shorter than the florets, and dissimilar glumes that are never reduced. *Trisetum irazuense* is distributed in Mexico, Costa Rica, Panama, Honduras, Colombia, Venezuela, Ecuador, and Peru (Hitchcock, 1927; Pohl, 1980; Hernández-Torres & Koch, 1988; Davidse et al., 1994; Jørgensen & Ulloa, 1994; Finot et al., 2004).

Additional specimens studied. ARGENTINA. **Chubut:** Lago Fontana, 10 Feb. 1932, *Castellanos s.n.* (BA, S). **Neuquén:** Los Lagos, Villa La Angostura, *Pedersen 1523* (CTES). **Río Negro:** Bariloche, Valle del Chollhuaco, Refugio Neumeyer, *Rúgolo de Agrasar et al. 12381* (CONC); Región montañosa cercana al Lago Nahuel Huapí, *Parodi 11827* (BAA); P.N. Nahuel Huapí, Cerro López, *Pérez Moreau 1949* (BA); Lago Nahuel Huapí, Cerro Catedral, *Cabrera 11511* (LP). **Tierra del Fuego:** Bahía Lapataia, 2 Feb. 1948, *Pérez Moreau & Guarrera s.n.* (BA); Valle de Tierra Mayor, *Ruiz Leal & Roig 15023* (MERL, BAA); Ushuaia, source gauche du Río Grande, 7 Mar. 1896, *Alboff s.n.* (CORD); Ushuaia, cerros alrededores de Ushuaia, *Grondona 5695* (BAA). CHILE. **IX Región:** Malleco, Cordillera de Las Raíces, *Matthei & Bustos 111* (CONC). **X Región:** Valdivia, Chihuio, Hito de Portezuelo Ipela, *Godoy 119* (CONC); Palena, Las Escalas, Futaleufú, *Hildebrand-Vogel 31* (CONC); Río Chico, Futaleufú, *Hildebrand-Vogel 45* (CONC). **XI Región:** Aysén, Reserva Forestal Mano Negra, *Schlegel 7194* (CONC); Reserva Forestal Mano Negra, *Schlegel 7187* (CONC); Prov. Coihaique, Sector Lago Palena, *Godoy, Hildebrand-Vögel & Vögel 3* (CONC); Parque Nacional Trapananda, *Schlegel 8070* (CONC); General Carrera, Estero Cofré, *Vogel 540* (CONC); Estero Cofré, *Vogel 519* (CONC); Río Ibáñez, *Vogel 5* (CONC); Capitán Prat, Villa O'Higgins, *Vogel s.n.* (CONC). **XII Región:** Magallanes, Punta Arenas, Minas de carbón, *Ricardi & Matthei 335* (CONC); Puerto Williams, Isla Navarino, Cerro Bandera, *Schlegel 8122* (CONC).

2. Trisetum flavescens (L.) P. Beauv., Ess. Agrostogr. 88, 153, t. 18, f.1. 1812. Basionym: *Avena flavescens* L., Sp. pl. 80. 1753. *Trisetaria flavescens* (L.) Baumg., Enum. Stirp. Transsilv. 3: 263. 1816. *Rebentischia flavescens* (L.) Opiz,

Lotos 4: 104. 1854, as synonym of *Trisetum flavescens* (L.) P. Beauv. TYPE: Herb. A. Van Royen no. 913.7–458 (lectotype, LINN-97.14, designated by Cope in Cafferty et al., Taxon 49(2): 247. 2000, not seen).

Perennial, caespitose; culms (20–)80–110 cm tall; nodes 2 to 5, glabrous. Leaf sheaths shorter than the internodes, glabrous or sparsely pilose below; ligule 0.5–2 mm long, truncate, ciliate, the dorsal surface glabrous; blades (3–)10–16 × 0.2–0.4 cm, flat, glabrous abaxially, scabrous and sparsely pilose adaxially. Panicles 5–18 × 2–8 cm, dense, lax, open or narrow, gold-yellow, shining. Spikelets 5–7(–8.5) mm, 2- to 4-flowered; rachilla ca. 1.2 mm long, pilose, with trichomes up to 1 mm long; glumes shorter than the florets, unequal; keel scabrous; first glume 2–4 × 0.1–0.2 mm, linear-lanceolate, narrow, 1-nerved, subulate, usually 1/2 as long as the second glume; second glume 4–6.6 × 1 mm, oval-lanceolate, 3-nerved; lemmas 4–6 mm long, glabrous, awned, somewhat scabrous toward the apex; apex 2-dentate to 2-aristulate; awn 5–9 mm long, borne on upper 1/3 or 1/4, geniculate and twisted toward the base; callus pubescent, the trichomes ca. 0.5 mm long; paleas a little shorter than the lemma, hyaline, 2-nerved, the nerves scabrous; apex 2-dentate to 2-setulate; lodicules bilobed at the apex; anthers 2–3 mm long; ovary glabrous. Caryopses 2–3 mm long, glabrous; endosperm liquid.

Chromosome number. $2n = 24, 28$ (Bolkhovskikh et al., 1969; Tsvelev, 1983; Dixon, 1995; Frey, 1992).

Distribution and habitat. A European species that was introduced from Europe in North and South America (Frey, 1992). In South America it occurs in the Chilean and Argentinean Patagonia and is an important forage plant (Nicora, 1978). Zuloaga et al. (1994) cited this species for Neuquén, Argentina.

Phenology. Flowering in December.

Illustrations. Hitchcock and Chase (1950: 291, fig. 393); Nicora (1978: 242, fig. 157 A–C).

Additional specimens studied. ARGENTINA. **Neuquén:** Península Panguinal, costa N Lago Nahuel Huapí, *Diem 463* (BAA); Nahuel Huapi, cultivated, *Gallinal, Aragone, Bergalli, Campal & Rosengurtt 5594* (US). GERMANY. Magdeburg, 23 June 1932, *Schwing s.n.* (CONC). U.S.A. **Washington:** Walla Walla, 31 May 1900, *Lechenby s.n.* (US).

3. Trisetum foliosum Swallen, Contr. U.S Natl. Herb. 29(6): 256. 1948. TYPE: Venezuela. Mérida: rocky slopes along stream above Laguna Mucubaji, toward Laguna Negra, 3625–3655 m, 21 July 1944, *J. A. Steyermark 57482* (holotype, US-1911640!; isotypes, MO-3846028!, MO-3873805 fragm. ex VEN!; VEN not seen, F-1216139!).

Perennial, with short rhizomes; culms glabrous, 35–80 cm tall; nodes glabrous, basal. Leaf sheaths sometimes with auricles, lower sheaths covered with short retrorse trichomes, the upper sheaths glabrous to puberulous; ligule 2–4 mm long, hyaline, oval to triangular, denticulate on the margins, the dorsal surface glabrous; blades 7–20 × 0.1–0.6 cm, flat; lower blades on culm densely pubescent, upper blades glabrous. Panicles 10–19 × 1–1.5 cm, lax, contracted, not spiciform, linear, purple; rachis glabrous. Spikelets 7–7.5 mm long, 2-flowered; pedicels 0.5–5 mm long, glabrous; rachilla 1–1.8 mm long, covered with trichomes 1–1.5 mm long; glumes subequal, the first glume a little shorter than the second glume, membranous; margins hyaline; keel scabrous near apex; apex acute; first glume 5.5–6.4 × 0.6–1.2 mm, oval-lanceolate, attenuate, 1-nerved; second glume 6.5–7 × 1–1.6 mm, oval, 3-nerved, almost equaling the spikelet in length; florets 6–6.7 × ca. 1 mm; upper floret shorter; lemmas glabrous, awned dorsally; apex bidentate, the teeth aristulate with projection of the intermediate nerves; awn 8–11 mm long, borne on the upper 1/3, at 2–2.5 mm from the apex, twisted at the base, curved or weakly geniculate, scabrous; callus obtuse, with trichomes 0.5–0.8 mm long; paleas ca. 4.5 mm long, shorter than the lemma, hyaline, 2-nerved, the nerves scabrous; anthers 1.2–1.5 mm long; lodicules 0.7–0.8 mm long, obovate, with 3 or 4 short apical teeth; ovary glabrous, the styles well apart. Caryopses not seen.

Distribution and habitat. *Trisetum foliosum* is endemic to Venezuela. It has been collected in páramos on rocky slopes and near streams and lakes, between 3500 and 3655 m.

Phenology. Flowering between November and July.

Comments. *Trisetum foliosum* resembles *T. flavescens* and *T. cernuum* in having lax panicles and spikelets with glumes shorter than the florets. It differs from *T. cernuum* in having subequal glumes, the first glume a little shorter than the second glume, the first glume never reduced, and the ovary is glabrous (glumes very unequal, the first glume conspicuously shorter than the second glume, the first glume sometimes reduced, and the ovary is hairy in *T. cernuum*). *Trisetum foliosum* differs from *T. flavescens* in having more contracted (1–1.5 cm wide) and purple panicles and longer ligules (2–4

mm long) versus open (2–8 cm wide) and gold-yellow panicles, and shorter ligules (0.5–2 mm long) in *T. flavescens*.

Additional specimen studied. VENEZUELA. **Mérida:** pass on the Mérida–Barinas Hwy., páramo above Laguna Grande and Universidad de Los Andes Experimental Station, *Davidse 3226* (US).

4. Trisetum irazuense (Kuntze) Hitchc., Proc. Biol. Soc. Wash. 40: 82. 1927. Basionym: *Calamagrostis irazuensis* Kuntze, Revis. Gen. Pl. 2: 763. 1891. TYPE: Costa Rica. Volcán Irazú, Waldregion, 3000 m, 24 June 1874, *C. E. O. Kuntze 2334* (holotype, NY-346300 ex Herb. Kuntze!).

Trisetum scabriflorum Hitchc., Contr. U.S. Natl. Herb. 24: 358. 1927. TYPE: Colombia. Cauca: collected below Pitayó, Río Palo Basin, Tierra Adentro, 2400 m, Feb. 1906, *H. Pittier 1435* (holotype, US-531631!).

Trisetum fournieranum Hitchc., Contr. U.S. Natl. Herb. 17: 326. 1913, new name for *Trisetum gracile* E. Fourn., Mexic. Pl. 2: 108. 1886, *nom. illeg.* TYPE: "San Luis de Potosí," *M. Virlet d'Aoust 1382* (lectotype, P!, designated by Finot et al., Ann. Missouri Bot. Gard. 91: 13. 2004; isotype, US-726971b fragment ex P!).

Perennial; caespitose; culms 75–100 cm tall, glabrous, up to 2 mm diam. on the lower internodes; nodes 3, glabrous. Leaf sheaths shorter or slightly longer than the internodes, glabrous or pubescent; basal sheaths pubescent; ligule 2–4 mm long, membranous, pubescent to densely pubescent, the apex truncate, dentate or ciliate; blades 20–30 cm × 2.5–6 mm, flat, glabrous or pubescent; upper blades 5–10 cm long. Panicles (7–)3–25 × (1–)2–5 cm, lax, narrow, yellow-green to deep green and purple; rachis glabrous to sparsely pubescent; the branches appressed and ascending. Spikelets 4–7(–9) mm long, 2- or 3-flowered; pedicels 2–7 mm long, glabrous to sparsely pubescent, sometimes scabrous; rachilla 1–1.7 mm long, covered with stiff trichomes, the trichomes 0.5–1 mm long; glumes very unequal, shorter than the florets; the keel scabrous on the upper half, the margins hyaline; first glume 2.5–5 mm long, narrow, linear, 1-nerved, acute at the apex, half as long as the spikelet; second glume 3.5–6.5 mm long, lanceolate to ovate-lanceolate, abruptly attenuate, 3-nerved, 3/4 as long as the spikelet; lemmas 4.3–6 mm long, 5-nerved, the nerves inconspicuous toward the base, strongly scabrous on the upper half, green and purplish toward the apex, sometimes with short trichomes toward the base; apex awned, hyaline, biaristate or toothed, the apical awns ca. 0.5 mm long, conspicuous; awn (2.5–)5.5–8.5 mm long, borne on the upper 1/3 or 1/4, straight or twisted and geniculate; callus obtuse, with short trichomes, the trichomes ca. 0.2–0.3 mm long; paleas 3.2–4.6 mm long, slightly shorter than the lemma, hyaline, 2-keeled, the keels scabrous on the upper half, 2-dentate to 2-awned at the apex; anthers (0.8–)1.2–1.8 mm long; lodicules ca. 0.7 mm long, bilobed at the apex, the lobes acute; ovary glabrous. Caryopses 2.2–3 mm long; endosperm soft.

Chromosome number. $2n = 28, 42$ (Hernández-Torres & Koch, 1988).

Anatomy and micromorphology. Hernández-Torres & Engleman (1995); Finot et al. (2004).

Distribution and habitat. *Trisetum irazuense* ranges from Mexico to Peru (Calderón de Rzedowski & Rzedowski, 2001; Finot et al., 2004). In South America it is found in Colombia, Venezuela, Ecuador, and Peru between 1500 and 3800 m.

Phenology. Flowering between November and August.

Illustrations. Pohl, W. (1980: 578, fig. 217 C).

Comments. *Trisetum irazuense* resembles *T. cernuum* in having lax, open panicles bearing long pedicellate spikelets with dissimilar glumes shorter than the florets. Anatomically both species have very similar characteristics in anatomical transverse section, and abaxial and adaxial epidermes. However, these two species are easily separated. *Trisetum irazuense* has strongly scabrous lemmas (relatively glabrous in *T. cernuum*) and a glabrous ovary (hairy in *T. cernuum*) (see additional comments under *T. cernuum*).

Additional specimens studied. COLOMBIA. **Bogota:** Peña, *Lindig 1862* (P). **Caldas:** Laguneta, Salento, *von Sneidern 3027* (S). **Santander:** Minas San Juan 5 km above California, *Robinson & Beltran 3041* (US). **Departamento del Valle:** Cordillera Central, vertiente occidental, Hoya del río Bugalagrande, Barragán, cerro de La Laguna, *Cuatrecasas 20847* (F); Cordillera Central, vertiente occidental, Hoya del río Bugalagrande, Loma de Barragán, desde La Parrilla a La Machuca, *Cuatrecasas 20680* (F). ECUADOR. **Carchi:** Hacienda La Esperanza, sector El Voladero, páramo de El Angel, *Dávalos 20* (US); 22 km SW of Tulcan on road to El Angel, *Peterson et al. 9146* (US); Valle de Maldonado, km 53 on the road Tulcán–Maldonado, *Holm-Nielsen et al. 5553* (S); Las Penas between La Rinconada and San Gabriel, *Asplund 7215* (S); above el Pun toward Tulcán, *Asplund 16868* (S). **Pichincha:** below San Juan, *Asplund 16093* (S); vicinity of Quito, *Asplund 6156* (S); Mt. Corazón, páramo, *Asplund 9686* (S); Nono, *Asplund 7441* (P, S); Reserva Geobotánica Pasochoa, *Laegaard 101414* (QCA); Pululagua, *Asplund 6733* (US). **Ríobamba:** Hacienda Toldo, Oct. 1891, *Sodiro s.n.* (P). **Azuay/Morona:** near the pass on road Sigsig–Gualaquiza, *Laegaard et al. 103031* (QCA). **Bolívar:** La Magdalena, *Asplund 8280* (P, S). **Tungurahua:** vicinity of Patate, Hacienda Leito, *Asplund 7978* (P). PERU. **Piura:** Prov. Huancabamba, 23 km E of Sondor, on road toward Tabacones, *Peterson & Refulio-Rodríguez 15135* (US). VENEZUELA. **Mérida:** entre Timotes y Chachopo, *Bur-*

kart & Tamayo 16733 (BAA). **Monagas:** Cerro Negro, above La Sabana de las Piedras, NW of Caripe, *Steyermark 62083* (F). **Sucre:** Cerro Turumuquire, north-facing slopes between La Trinidad and zone of cloud forest, *Steyermark 62488* (F).

Trisetum subg. **Trisetum** sect. **Trisaetera** Asch. & Graebn., Syn. Mitteleur. Fl. 2: 270. 1895. TYPE: *Trisetum spicatum* (L.) K. Richt.

5. Trisetum ambiguum Rúgolo de Agrasar & Nicora, Bol. Soc. Argent. Bot. 25: 468. 1988. TYPE: Argentina. Prov. Santa Cruz: Dpto. Güer Aike, Ea. Sofía, Secc. Cuadrado, 5 km al S de Est. Punta del Monte, 350 m, 51°41′S, 71°18′W, 12 Feb. 1978, *O. Boelcke, D. Moore & F. Roig 3119* (holotype, BAB not seen; isotype, SI!).

Perennial, with short rhizomes; culms 12–34 cm tall, with short, retrorse trichomes below the inflorescence. Leaf sheaths glabrous or pubescent; ligule 1–2.5 mm long, denticulate, laciniate, the dorsal surface glabrous; blades 40–50 × 1.5–2 mm, short, flat to conduplicate, scabrous on the margins, glabrous to pilose abaxially, scabrous-pubescent to pilose adaxially. Panicles 4–7.5 × 1–1.5 cm, spiciform, dense; rachis pilose. Spikelets ca. 6 mm long, 1-flowered; pedicels scabrous; rachilla ca. 1.5 mm long, pilose with trichomes 1.5 mm long; glumes longer than the floret isomorphic; first glume 5–5.5 × ca. 0.5 mm, equal or slightly shorter than the floret, and slightly shorter and narrower than the second glume, lanceolate to oval-lanceolate, equaling or slightly shorter than the florets, 1-nerved; second glume 5–5.5 × ca. 0.8 mm, slightly longer or equaling the floret, lanceolate to oval-lanceolate, 3-nerved; florets 4–5 mm long; lemmas glabrous, scabrous toward the apex, 5-nerved, the nerves conspicuous toward the apex, awned dorsally; apex hyaline with the intermediate and marginal nerves prolonged as 4 short awns; awn 4–5 mm long, borne on the upper 1/3, strongly twisted and curved; callus obtuse, with trichomes ca. 0.5 mm long; paleas 3–3.5 mm long, shorter than the lemma, 2-nerved, the nerves scabrous toward the apex; flowers cleistogamous; anthers 0.5–0.8 mm long; lodicules ca. 0.8 mm long, minutely bilobed near the apex; ovary with 1 to several curved trichomes at the apex. Caryopses ca. 2.5 mm long, pubescent at the apex; endosperm dry.

Distribution and habitat. Endemic to southern Argentina and Chile (Zuloaga et al., 1994; Finot, 2002). In Argentina it is found in Santa Cruz and Tierra del Fuego, between 51°S and 53°55′S (Rúgolo de Agrasar & Nicora, 1988). In Chile it grows in Región XII, Prov. de Ultima Esperanza, between 50°S and 51°S, and between 500 and 900 m.

Phenology. Flowering between January and February.

Illustrations. Rúgolo de Agrasar and Nicora (1988: 469, fig. 2A–K).

Comments. Trisetum ambiguum is closely related to *T. spicatum* var. *cumingii* and differs from the latter by having 1-flowered spikelets, isomorphic glumes, the awn several times curved, and the ovary and caryopsis with a few trichomes. *Trisetum spicatum* var. *cumingii* has 2- or 3-flowered spikelets, unequal glumes, a geniculate awn, and a glabrous ovary and caryopsis.

Additional specimens studied. ARGENTINA. **Santa Cruz:** Güer Aike, Valle Superior Río Turbio, *Ambrosetti & Méndez 29875* (MERL); Valle Superior Río Turbio, *Ambrosetti & Méndez 29883* (MERL); Estancia La Carlota, sección San Elías, *Roig et al. 103* (SI). **Tierra del Fuego:** Norte de Río Grande, Ea. María Behety, *Soriano 4847* (BAA, paratype); Castillo, 30 Jan. 1942, *Castellanos s.n.* (BA); Río Grande, 1 Mar. 1917, *Bonarelli s.n.* (SI); Cerro Mesa, 31 Jan. 1942, *Castellanos s.n.* (BA). CHILE. **XII Región:** Prov. de Ultima Esperanza, Sierra de los Baguales, La Cumbre, Campo de La Tropilla, *Landero 790* (CONC); Sierra de los Baguales, Cerro Santa Lucía, 15 Jan. 1985, *Arroyo s.n.* (CONC 85160); Sierra del Toro, *Arroyo et al. 9276* (CONC); Sierra del Toro, 10 Feb. 1992, *Arroyo et al. s.n.* (CONC 92112).

6. Trisetum andinum Benth., Pl. Hartw. 261. 1847. *Trisetum spicatum* var. *andinum* (Benth.) Louis-Marie, Rhodora 30: 239. 1929. *Trisetum spicatum* (L.) K. Richt. subsp. *andinum* (Benth.) Hultén, Svensk Bot. Tidskr. 53: 224. 1959. TYPE: Ecuador. Hacienda de Antisana, *C. T. Hartweg 1449* (holotype, K not seen; isotypes, P!, BAA-3345!, US fragm. ex P-STEUD!).

Perennial, caespitose, velvety, sometimes with short rhizomes; culms (9–)20–42 cm tall, erect, robust, up to 4 mm diam. near the base, pubescent almost all its length, densely hairy below the panicle; nodes 1, basal. Lower leaf sheaths ca. 20 cm long, lax, pilose; upper sheaths 5–10 cm long, pilose; ligule 0.5–2 mm long, truncate, ciliate on the margin, dorsal surface densely pilose; blades 3–15 cm × 2–3.5 mm, flat, pilose abaxially, sparsely pilose adaxially; margins of lower blades usually involute. Panicles 3–6 × 1–2.5 cm, spiciform, very dense, ovate, no more than 3 times as long as wide, included or exerted in the upper sheath, tinged with gold and purple, rounded at the apex; rachis pubescent; spikelets 5–7 mm long, 2- or 3-flowered; rachilla 0.6–0.8 mm long, with a few stiff trichomes, the trichomes as long as the rachilla;

glumes equaling or longer than the florets, sometimes only the first glume longer than the florets, unequal; first glume 3.5–6 × 0.5–0.6 mm, shorter and narrower than the second glume, linear-lanceolate, attenuate, 1-nerved; second glume 4–7 × 0.8–1 mm, oval, 3-nerved, rarely shorter than the florets; florets 5–5.5 mm long; lemma scabrous or covered with very short trichomes giving a velvety texture, dorsally awned, purple and green, the apex 2-aristulate with the projection of the intermediate nerves, the mucros 0.4–0.5 mm long; awns 3.5–4.5 mm long, inserted on upper 1/3, usually not geniculate nor twisted but diversely curved, scabrous; callus obtuse, with few short trichomes, the trichomes ca. 0.2 mm long; paleas 3.7–6 mm long, shorter than the lemma, hyaline, 2-nerved, the nerves scabrous; apex 2-dentate, sometimes short-mucronate; anthers 0.7–1 mm long; lodicules ca. 0.8 mm long, hyaline, 2-lobulate at the apex; ovary glabrous. Caryopses 2.2–2.5 × ca. 0.5 mm, glabrous.

Distribution and habitat. Endemic to Ecuador, *Trisetum andinum* is found between 3900 and 4700 m, in páramo and superpáramo vegetation, on volcanic soil.

Phenology. Flowering between December and September.

Comments. *Trisetum andinum* resembles *T. spicatum*. It has been treated as a synonym of *T. spicatum* by Jørgensen and Ulloa (1994), Renvoize (1998), and Jørgensen and León-Yañez (1999). Hitchcock (1927) accepted *T. andinum* as a good species, but it was later treated by Louis-Marie (1928, 1829) as a variety and by Hultén (1959) as a subspecies of *T. spicatum*. The most remarkable differences between *T. andinum* and *T. spicatum* are the shape of the panicles and the hairiness of the plant. *Trisetum andinum* is totally covered with a dense indumentum (*T. spicatum* is glabrous except below the panicle). *Trisetum andinum* possesses oval, dark purple panicles, usually no more than 2 or 3 times longer than wide (*T. spicatum* possesses panicles green or purple, narrow, more than 3 times longer than wide). *Trisetum andinum* possesses glumes as long as the florets or the second glume longer than the florets (glumes shorter than the florets in *T. spicatum*). The isotype of *T. andinum* at P has both glumes longer than the florets (first glume 6 × 0.8 mm, second glume 7 × 0.8 mm).

Additional specimens studied. ECUADOR. **Cotopaxi:** P.N. Cotopaxi, *Ehrenburg 49* (QCA); Volcán Cotopaxi, *Sklenar & Kosteckova 80–12* (QCA); Páramos del Cotopaxi, *Roig 12356* (MERL); Cotopaxi, SW slope of the volcano, *Asplund 7499* (S). **Ibambura:** NE side of Cayambe Mountain, 10 Dec. 1961, *Cazalet & Pennington 5740* (US); W side of Mount Cayambe, in páramos, *Little & Paredes 6832*[1/2] (US). **Pichincha:** Pichincha, *André 3907* (US); Summit of Pichincha, *Jameson s.n.* (US-868479); Mt. Pichincha, near Quito, *Hitchcock 21059* (US); 36 km E of El Refugio, on the SW slope of Volcán Cayambe, *Peterson, Judziewicz & King 9075* (US); Faldas SE Volcán Guagua-Pichincha, *Novcak & Marcillo 79* (QCA); Guagua Pichincha, E slopes of the volcano, *Sklenar & Kosteckova 812* (QCA); Guagua Pichincha, *Asplund 7401* (S, US); W parts of Rucu Pichincha massif, summit and upper W slopes of Padre Encantado, *Molau & Eriksen 3297* (QCA); Guagua Pichincha, *Harling 4537* (S); Lloa-Guagua Pichincha km 10, *Laegaard, Romoleroux & León 102731* (QCA); sommet du Pichincha, Oct. 1856, *J. Remy s.n.*, (P); Pichincha, *Benoist 2389, 4389* (P); monte Rucu Pichincha, *Holmgren 553* (S). **Pichincha/Napo:** Antisana, *Ehrenburg 137* (QCA); Volcán Antisana, between Campamento IMAP and Laguna Micacocha, *Laegaard 101604* (QCA).

7a. Trisetum barbinode Trin. var. **barbinode,** Linnaea 10(3): 300. 1836. TYPE: Chile Austral. Andes de Antuco, 1828, *E. Poeppig s.n.* (holotype, LE-TRIN-1886.01!; isotypes, US-81770 ex W!, US-868486 fragm. ex LE-TRIN!, BAA-3351 fragm. ex LE-TRIN!, SGO-73101 photo ex LE-TRIN!, W not seen).

Perennial; culms (18–)25–45(–55) cm tall, sometimes with short rhizomes, pilose or sericeous below the panicle, the trichomes first antrorse, then retrorse; nodes 1 or 2, basal, pubescent. Leaf sheaths glabrous; ligule 0.5–2 mm long, truncate, dentate-ciliate, dorsally glabrous; blades (2–)10–15 cm × 2–3(–5) mm, flat, soft, glabrous, margins and adaxial surface scabrous. Panicles 4.5–15 × 0.8–2.5(–3) cm, pale green, contracted, dense, linear-lanceolate to oval; rachis pubescent, the trichomes up to 1.5 mm long; spikelets 6–8(–11) mm long, 2- or 3-flowered; pedicels up to 5 mm long, pubescent; rachilla 1–2 mm long, pubescent, the trichomes up to 3 mm long; glumes unequal, with hyaline margins, the apex shortly aristulate or acute, the keel scabrous on the upper half, both glumes or only the second glume longer than the florets; first glume (5.5–)6.5–8.5 × 0.5–0.9 mm, slightly shorter and narrower than the second glume, linear-lanceolate, 1- or 3-nerved, usually equaling the first floret, sometimes longer; second glume 6.5–10 × 0.7–1.2 mm, lanceolate, 3-nerved; florets (5–)6.5–7.5 × (0.5–)0.8–1 mm; lemmas pubescent, dorsally awned, the apex biaristulate with apical awns 0.5–1 mm long; awn (2–)6.5–10(–14) mm long, curved or geniculate, not twisted; callus obtuse, pubescent, the trichomes 1.5–3 mm long; paleas (4–)5–6.5 mm long, shorter than the first lemma, equal or longer than the lemma in the second or third floret, hyaline, 2-nerved, the nerves scabrous, the apex bi-

dentate, the teeth 2-setulate; anthers (0.7–)1–1.6 mm long; lodicules 0.7–1 mm long, 2- or 3-lobate at the apex; ovary glabrous or with a few short trichomes at the apex. Caryopses 2.5–3.5 mm long, glabrous or with few trichomes at the apex; endosperm liquid.

Distribution and habitat. Endemic from central-southern Chile and Argentina, it is distributed along the Cordillera de los Andes, between 36°S and 41°S. In Argentina, *T. barbinode* var. *barbinode* grows in Neuquén, Río Negro, and Chubut, and in Chile between the Regions VII and IX, usually between 550 and 3500 m, on volcanic soils.

Phenology. Flowering between January and March.

Illustrations. Nicora (1978: 256, fig. 165A–C).

Comments. Morphologically, *Trisetum barbinode* var. *barbinode* is characterized by having contracted, pale green panicles with large spikelets 6–8(–11) mm long, hairy lemmas, and 3-nerved glumes longer than the florets. *Trisetum barbinode* resembles other taxa with hairy lemmas, such as *T. sclerophyllum* and *T. hirtiflorum*. Due to the variation in the shape, color, and size of the panicle and the length of the spikelets and glumes, it is often extremely difficult to distinguish among these three species. *Trisetum hirtiflorum* resembles *T. barbinode* s. str., and the only difference between these two species is the presence of a few short hairs at the apex of the ovary and caryopsis in *T. hirtiflorum*. According to Nicora (1978), *T. hirtiflorum* has shorter and narrower panicles and more rigid leaves than *T. barbinode*. However, these characters are so variable that recognition of these two species is nearly impossible. Louis-Marie (1929) first treated *T. hirtiflorum* as a variety of *T. barbinode*.

The close relationship between *Trisetum sclerophyllum* and *T. barbinode* was first observed by Louis-Marie, as it is clear from the annotation he made on the type deposited at US: "*T. barbinode* var. *sclerophyllum*" signed "*Lalonde.*" However, Louis-Marie (1928, 1929) did not include this combination or the Hackel binomial in his treatment of genus *Trisetum*. This type fragment at US from W contains only a fragment of the panicle. The spikelets are 2-flowered; the glumes are nearly equal and longer than the florets, the first glume 6–8 × 0.6–0.7 mm, the second glume 7–8 × 0.7–1 mm, and both are 3-nerved, with scabrous keel, hyaline margins, and hyaline, aristulate apex. The lower floret is ca. 5 mm long and the lemmas are pubescent, with a bi-aristulate apex, with apical awns up to 1 mm long. The dorsal awn (6–8 mm long) is borne on the upper 1/3 of the lemma. On the basis of this type fragment at US it is not possible to distinguish *T. sclerophyllum* from *T. barbinode* Trin. The varietal status for *T. sclerophyllum* was also suggested by Parodi since there is an annotation label on the type fragment deposited at BAA with his script. This, also, was never published.

Additional specimens studied. ARGENTINA. **Neuquén:** Catán Lil, Sierra del Chachil, *Rúgolo de Agrasar 451* (BAA); Loncopué, Cajón Chenque Pehuén, *Rúgolo de Agrasar & Agrasar 148* (BAA); Los Lagos,Villa La Angostura, cerro Belvedere, *Rúgolo de Agrasar 1234-1* (SI); P.N. Lanín, Volcán Huanquihue, al W del Lago Currhué, *Eskuche & Klein 1520-7* (CORD); a 5 km de Las Ovejas, camino a las lagunas Epu-Lauquén, *Boelcke 10764* (CONC ex BAA); Baños Calientes, Río Valvarco, *Boelcke et al. 11452*$^{1/2}$ (BAA); entre Lagunas Epu-Lauquén y Cajón Lumavia, *Ragonese 234* (BA); Lagunas Epu-Lauquén, *Boelcke et al. 10927* (CONC ex SI). **Río Negro:** P.N. Nahuel Huapi, Cuenca Río Manso Superior, camino a Ventisqueros del Tronador, *Diehl & Bravo 10843* (BA). CHILE. **VII Región:** Talca, Laguna del Maule, *Schlegel 3475* (CONC); Laguna del Maule, *Schlegel 3537* (CONC). **VIII Región:** Ñuble, Termas de Chillán, *Jaffuel 1806-b* (SGO), 9 Jan. 1949, *Pfister s.n.* (CONC); Baños de Chillán, Jan. 1877, *F. Philippi s.n.* (SGO); Baños de Chillán, *Philippi 218* (SGO); Termas de Chillán, Faldeos del Volcán Chillán, *Ricardi 5604* (CONC); Termas de Chillán, *Philippi 229* (SGO); Termas de Chillán, zona de las fumarolas, *Finot & Baeza 2069* (CONC); entre Valle Hermoso y Termas de Chillán, *Finot & Baeza 2070* (CONC); Refugio Club Andino de Chillán, Shangri-La, *Garaventa 4681* (CONC); Bío-Bío, Laguna del Laja, *Fabris & Crisci 7608* (LP); Lago Laja, 2 Feb. 1968, *Zoellner s.n.* (ZOELLNER); Laguna del Laja, *Ricardi & Marticorena 5812/1973* (CONC), *Burkart 27451* (CONC ex SI); faldeos del Volcán Antuco, frente a la laguna del Laja, *Ricardi & Marticorena 5723/1884* (CONC); Las Lagartijas, *Finot & Baeza 2073* (CONC). **IX Región:** Malleco, Lonquimay, Estepa cerca Laguna Icalma, 10 Jan. 1947, *Pfister s.n.* (CONC); Curacautín, Paso Las Raíces, 14 Feb. 1992, *Zoellner s.n.* (ZOELLNER); Termas de Río Blanco, *Pfister s.n.* (CONC); Icalma, cerro del lado sur, *Pfister s.n.* (CONC); Cautín, Volcán Llaima, Refugio Cautín, *Montero 4497, 4487* (CONC); Volcán Llaima, *Gunckel 12426* (CONC), *Sparre 4873* (S); Villarrica, Tromén, Límite Chileno-Argentino, *Ricardi & Matthei 3, 15* (CONC); Curarrehue, 29 Dec. 1946, *Cañulaf s.n.* (CONC).

7b. Trisetum barbinode var. **hirtiflorum** (Hack.) Louis-Marie, Rhodora 30: 240. 1929. Basionym: *Trisetum hirtiflorum* Hack., Repert. Spec. Nov. Regni Veg. 10 (243–247): 169. 1911. TYPE: Chile. *C. Reiche s.n.* (holotype, W not seen; isotypes, BAA!, SGO fragm. & photo ex W!, US fragm. ex W!).

Panicles 4–5 cm long, gold-purple, spiciform, dense. Leaf blades soft. Second glume 5–8 mm long; ovary with short trichomes on the apex.

Distribution and habitat. Southern Chile (VIII Región) and Argentina (Neuquén) between 500 and 2000 m (Nicora, 1978).

Phenology. Flowering in January.

Additional specimen studied. CHILE. **VIII Región:** Prov. Ñuble, Termas de Chillán, por la loma de las fumarolas, 17 Jan. 1945, *Pfister s.n.* (CONC, SGO).

7c. Trisetum barbinode var. **sclerophyllum** (Hack.) Finot, comb. nov. Basionym: *Trisetum sclerophyllum* Hack., Anales Mus. Nac. Hist. Nat. Buenos Aires 21: 108. 1911. TYPE: Argentina. Chubut: Dpto. Languiñeo, Región del río Corcovado, 20 Jan. 1902, *Illin 148* (holotype, W ex Stuckert Herb. Arg. 17991 not seen; isotypes, BAA-3414!, US-91365 fragm. ex W!).

Culms 18–30 cm tall. Leaf blades stiff. Panicles (2–)3–5(–8) cm long, gold-purple, spiciform, dense. Glumes subequal in width; second glume 5–8 mm long; ovary glabrous.

Distribution and habitat. Endemic to Argentina, *T. barbinode* var. *sclerophyllum* occurs along the Cordillera de Los Andes in Mendoza, Neuquén, Río Negro, and Chubut, between 32°S and 42°S latitudes and between 1170 and 3500 m.

Phenology. Flowering between January and March.

Additional specimens studied. ARGENTINA. **Mendoza:** Las Heras, Faldeo SSW morrena cerro Tolosa, *Boelcke et al. 9778* (MERL, CONC); San Rafael, Cerro Volcán Overo, *Roig 1* (MERL); alto valle de Calmuco, *Burkart et al. 13930* (BAA ex SI); alto valle del Atuel, *Paci 15731* (BAA, MERL); Laguna Atuel, *Ruiz Leal 16886* (MERL); Tupungato, Las Tres Quebradas, *Ruiz Leal 3616* (MERL). **Neuqén:** Sierra de Cochicó, *Boelcke et al. 14083* (BAA, CONC ex SI); Ñorquín, entre Las Maquinitas y Copahue, *Calderón & Rúgolo 57* (BAA); Copahue, *Calderón & Rúgolo 72* (BAA); Pino Hachado, Feb. 1920, *Hauman s.n.* (BA), *Parodi 2700* (BAA); Paso Pino Hachado, en el hito, *Nicora 7432* (BAA); San Martín de Los Andes, P.N. Lanín, arroyo Rucu-Leufú, *Correa et al. 5647* (CONC ex BAB); P.N. Lanín, Cerro Chapelco, 12 Feb. 1961, *León & Calderón s.n.* (BAA); Cerro Chapelco, *Schajowski 86, 133, 134, 178* (BA), *Cabrera & Crisci 19145* (LP), *Cabrera et al. 23024* (LP); Lago Lácar, Cerro Malo, *Rúgolo de Agrasar 315, 318* (BAA); Cerro Repollo, Estancia Meliquina, *Rúgolo & Agrasar 570* (BAA); Los Lagos, Villa La Angostura, cerro Belvedere, *Rúgolo de Agrasar 1234–2* (SI); Pto. Manzano, en la cima del cerro O'Connor, *Diem 3229* (BAA); P.N. Nahuel Huapi, Filo refugio Cerro Colorado a Cerro, *Boelcke & Correa 6959* (BAA); mallines en ladera Cerro, *Boelcke & Correa 6964* (BAA). **Río Negro:** Cerro de Las Hormigas, *Hosseus 559, 560* (CORD); P.N. Nahuel Huapí, Cerro Catedral, *Cabrera 19754* (LP), *Parodi 15321* (BAA), *Pérez Moreau s.n., 1949* (BA). **Prov. Chubut:** Dpto. Futaleufú, Esquel, La Hoya, *Cabrera et al. 23170* (LP); P.N. Los Alerces, Lago Futalaufquén, *Soriano 4352* (BAA).

8a. Trisetum caudulatum Trin. var. **caudulatum,** Linnaea 10(3): 300. 1836. *Koeleria caudulata* (Trin.) Griseb., Abh. Konigl. Ges. Wiss. Gottingen 24: 292. 1879. TYPE: Chile. Andes Chile boreal, *E. F. Poeppig s.n.* (holotype, LE-TRIN-1887.01!; isotype, BAA-3364 fragm. ex LE-TRIN!).

Trisetum chromostachyum E. Desv., Fl. Chil. 6: 350. 1854. TYPE: Chile. Santiago, in arvis, Jan. 1829, *C. Gay s.n.* (holotype, P!; isotypes, CONC-148153 fragm. ex P!, SGO fragm. ex P!, US fragm. ex P-DESV-156!, US fragm. ex P-GAY!).

Trisetum heteronymum Steud., Syn. Pl. Glumac. 1: 229. 1854. TYPE: Chile. "Rancagua, in pascuis et ad fossas," Oct. 1828, *C. L. G. Bertero 53* (published as *Bertero 83*) (holotype, P-STEUD-437!; isotypes, SGO fragm. ex P!, US fragm. ex P!; US fragm. ex P!).

Trisetum variabile E. Desv., Fl. Chil. 6: 351. 1854. *Trisetum variabile* var. (alpha) *flavescens* E. Desv., Fl. Chil. 6: 351. 1854. TYPE: (Chile) Valparaíso, 1829, *C. L. G. Bertero 998* (lectotype, designated here, P!; isotypes, BAA-3422 fragm. ex P!, SGO fragm. ex P!, US fragm. ex P!, US fragm. ex P-STEUD-440!).

Trisetum variabile var. *virescens* E. Desv., Fl. Chil. 6: 351. 1854. TYPE: Chile. Prov. Valdivia, In herbosis Guanegue, Feb. 1889, *C. Gay s.n.* (lectotype, designated here, P!; isotypes, BAA-3423 fragm. ex P!, CONC fragm. ex P!; SGO fragm. ex P!, US fragm. ex P!).

Trisetum malacophyllum Steud., Syn. Pl. Glumac. 1: 229. 1854. non Phil., Anales Univ. Chile 48: 566. 1873. TYPE: (Chile) Valparaiso, "*Festuca* nr. 997 Hbr. Bertero, In sylvaticis calidis Collinum loco dicto La Laguna," Oct. 1829, *C. L. G. Bertero 997* (lectotype, designated here, P!; isotypes, GH not seen, SGO fragm. ex P!).

Trisetum splendidulum Steud., Syn. Pl. Glumac. 1: 229. 1854. TYPE: Chile. "*Festuca*" *C. L. G. Bertero 996* (holotype, P-STEUD-441!; isotypes, BAA-3416 fragm. ex P!, CONC fragm. ex P!, SGO fragm. ex P!, US fragm. ex P!).

Trisetum chiloense Phil., Linnaea 29: 93. 1858. *Trisetum variabile* E. Desv. var. *chiloense* (Phil.) Louis-Marie, Rhodora 30: 240. 1928. TYPE: Chile. "in pascuis insulae Chiloé, ad Castro" *C. Gay 147* (holotype, SGO-PHIL-215!; isotypes, BAA-3371 ex SGO!, US fragm. ex SGO-PHIL-215 & photo!).

Trisetum monticola Phil., Linnaea 33: 291. 1864. TYPE: Chile. Prope Santiago, in andibus, Nov. 1861, *R. A. Philippi s.n.* (holotype, SGO-PHIL-227!; isotypes, SGO-37049!; US fragm. & photo ex SGO-PHIL-227!).

Trisetum ochrostachyum Phil., Linnaea 33: 290. 1864. TYPE: Chile. "E Valdivia attuli," *R. A. Philippi s.n.* (holotype, SGO-PHIL-220!; isotype, SGO-37062!).

Trisetum vidalii Phil., Anales Univ. Chile 94: 27. 1896. *Trisetum variabile* E. Desv. var. *vidalii* (Phil.) Louis-Marie, Rhodora 30: 240. 1929. TYPE: Chile. "Ad ostium fluminis Maullín," 41°30'S, *Franc. Vidal Gormaz s.n.* (holotype, SGO 37066!; isotypes, BAA-3424 ex SGO!, BAA-3425 ex SGO!; SGO-PHIL-231!, US fragm. & photo ex SGO-PHIL-231!; US photo ex SGO-37066!).

Trisetum lechleri (Steud.) Nicora, Fl. Patag. 3: 252. 1978. Basionym: *Koeleria lechleri* Steud., Syn. Pl. Glumac. 1: 294. 1854. TYPE: Chile. X Región: Arique, *W. Lechler 311* (holotype, P-STEUD-175!; isotype, US fragm. ex P!).

Perennial, sometimes with short rhizomes; culms 30–80 cm tall, glabrous, the upper internode usually very long; nodes 2 or 3, pubescent. Leaf sheaths 60–150 mm long, shorter than the internodes, pubescent; ligule 1–4 mm long, truncate to obtuse, dorsally glabrous or pilose, margins ciliate; blades 5–20 cm × 0.2–5 mm, flat to conduplicate, soft, pubescent. Panicles (4–)6–15 cm × 1–4 mm, contracted to spiciform, interrupted or not, usually dense, the lower branches 2–3 cm long, green, sometimes slightly purple, shining; rachis glabrous to scabrous. Spikelets 5.5–9 mm long, 2- to 4(to 5)-flowered, open at the apex; pedicels 1–4 mm long, scabrous; rachilla 0.7–1 mm long, pubescent, the trichomes up to 1.5 mm long; glumes shorter than the florets, unequal, aristulate at the apex or acute; first glume 3–6 × 0.3–0.5 mm, 1(or 3)-nerved, linear-lanceolate, attenuate; second glume 4–8 × 0.8–1.1 mm, 3(or 5)-nerved, oval-lanceolate to oval; florets 6.5–9.5 × 0.6–0.8 mm; lemmas linear-lanceolate, somewhat rounded on the back, glabrous, awned dorsally, dorsally scabrous; apex biaristulate, apical awns up to 1 mm long; awn borne on the upper 1/3 or 1/4 ca. 2–3.5 mm from the apex, geniculate, curved, weakly twisted, scabrous; callus pubescent, the trichomes 0.1–0.5 mm long; paleas 4.5–6.5 mm long, hyaline, 2-nerved, the nerves scabrous; 2-setulate; anthers (0.7–)1.2–1.7 mm long; lodicules 0.6–1.4 mm long, bilobed at the apex, the lobes acute; ovary glabrous. Caryopses ca. 4 × 0.6–0.7 mm, glabrous; endosperm liquid.

Chromosome number. $2n = 42$ (Baeza et al., 2001).

Distribution and habitat. *Trisetum caudulatum* var. *caudulatum* grows in Argentina (Neuquén, Río Negro, and Chubut) and Chile (Region II to XII) in prairies, woods, and heath along roadsides, frequently in sandy soils between 10 and 2200 m. Marticorena et al. (1998) reported the species for Isla Robinson Crusoe (Masatierra), Archipiélago de Juan Fernández, Chile.

Phenology. Flowering between October and March.

Illustrations. Nicora (1978: 251, fig. 164A–E).

Comments. The type of *Trisetum caudulatum* is represented in the Trinius Herbarium (LE-TRIN) by a fragment containing four spikelets (Nicora, 1978). One spikelet of this type is housed at BAA-3364 annotated by Parodi on 31 Jan. 1936, who wrote "La especie está representada en Leningrado por 4 espiguillas en un pequeño sobre (Nicora, 1978). No trae datos. El nombre bajo el cual figura es *T. caudulatum.*" The spikelet in BAA is 5.5 mm long, contains two florets with glumes unequal, shorter than the florets and each glume has a short awn at the apex. The first glume is 3.5 mm long, 1-nerved, lanceolate and the second glume is 4 mm long, 3-nerved, oval-lanceolate. The lemma is glabrous, 2-aristulate at the apex, awned on the upper 1/3 and the palea is shorter than the lemma in both florets. On the basis of the characters seen in the type specimens of *T. variabile* and *T. vidalii* at P, and the original Latin descriptions of the species, it is not possible to distinguish *T. variabile* and *T. vidalii* from *T. caudulatum.*

In reference to *Deschampsia lasiantha* (= *Trisetum preslei*), *T. andicola* (= *Trisetum longiglume*), *T. andinum*, *T. biforum* (= *Trisetum dianthemum*), *T. hirsutum* (= *Trisetum phleoides*), *T. malacophyllum* (= *Trisetum spicatum* var. *cumingii*), *T. chiloense*, *T. ochrostachyum*, *T. monticola*, *T. variabile*, and *T. vidalii* (all five species = *Trisetum caudulatum* var. *caudulatum*), the disposition of the R. A. Philippi collections has been a logistic problem for agrostologists for over 80 years. After her visit to Vienna in 1922, Agnes Chase indicated in an unpublished report (1923, Agnes Chase memorandum to the Bureau of Plant Industry, original at US!) on Edward Hackel's unpublished "Report on Grasses of Chile, 1920" (copy at US!), that Philippi's grass types were loaned to Hackel in Vienna by Philippi via K. F. Reiche (Herb. Mus. Nat. Chile, SGO), after these were returned from US to SGO. The US photographed the entire herbarium and retained fragments of most of the collections including types. Chase (1923, unpublished) noted that Hackel's annotated copy of Reiche's list of the Philippi collections was sent by Hackel to Reiche in Santiago de Chile in 1914. Reiche replied that he was leaving Chile for Mexico, and Hackel never heard from him again. The specimens were never returned to SGO and remain at W stamped "Herb. Hackel" (verified by Bruno Wallnöfer, pers. comm. with RJS, 2001).

Louis-Marie (1929: 240) created the new name *Trisetum variabile* var. *intonsum* to replace the illegitimate *T. variabile* var. *virescens* (Nees ex Steud.) Macloskie (Macloskie, 1904: 206; not *T. variabile* var. *virescens* E. Desv. (Desvaux, 1854: 351)), based on *T. virescens* Nees ex Steud., a plant described for India and placed in *Helictotrichon* by Henrard (1940) and in *Arrhenatherum* by Potztal (1968). Thus, *T. variabile* var. *intonsum* Louis-Marie is not a species from the New World.

Steudel (1853–1855) described *Trisetum heteronymum* with a variety (Variat: statura et omnibus partibus minoribus, spiculis trifloris, *Bromus* nr. 117, Bert., Chili). In P, BAA, and SGO there exists a specimen designated as *T. heteronymum* Steud.

var. *minor triflora*. This name is not a valid name, and the specimen is *Bertero 116*, not *Bertero 117* as the protologue indicates. These specimens were determined to be synonyms of *T. caudulatum*.

Additional specimens studied. ARGENTINA. **Chubut:** Lago Futalaufquén, en la cascada, *Krapovickas 3933* (SI); P.N. Los Alerces, Lago Cisne, *Roquero 452* (BA); Carrenleufú, *Illin s.n.* (LP); Pampa Chica, *Soriano 2490* (BAA); Lago Futalaufquén, claros del bosque de coigüe y ciprés, *Burkart 19905* (BAA); P.N. Los Alerces, Río 2, *Lahitte & Roquero 363* (BA); Corcovado, *Illin s.n.* (LP); Cerro Leleg, 14 Jan. 1949, *Pérez-Moreau s.n.* (BA). **Neuquén:** Lago Guillén, 28 Dec. 1937, *Kalela s.n.* (S); San Martín de Los Andes, *Bridarolli 2147* (LP 39146); San Martín de Los Andes, *Dawson 1285* (LP); P.N. Lanín, Lago Lácar, camino a Angostura, 17 Feb. 1961, *León & Calderón s.n.* (BAA); Isla Victoria, *Corte 34* (LP); Nahuel Huapí, Puesto Pañuelo, 18 Jan. 1930, *Offermann s.n.* (BAA); Fuerte Chacabuco, *Parodi 15611* (BAA); Parque Nacional Lanin, Arroyo Grande, S.L. Lacar, *Eskuche & Klein 316* (CTES); Parque Nac. Lanin, Pampa Hui Hui, *Eskuche & Klein 1417–27* (CTES); Nahuel Huapí, F. Chacabuco, *Vellerini 297* (BAA); Los Lagos, Villa La Angostura, Lago Nahuel Huapí, bahía próxima a Península Cumelén, *Rúgolo 1188* (CONC); Los Lagos, Villa La Angostura, cerro Bayo, *Rúgolo 1283* (CONC); Lago Epulafquén, *Dawson & Schwabe 2481* (BAA); P.N. Lanín, Lago Paimún, *Lahitte, Roquero & López 486* (BA); P.N. Lanín, San Martín de Los Andes, *Lahitte, Roquero & López 67* (BA); P.N. Lanín, San Martín de Los Andes, Lago Lácar, Quila-Quina, *Roquero 326* (BA); P.N. Lanín, Lago Lácar, Pucará camino a Angostura, *León & Calderón 1285* (BAA). **Río Negro:** Lago Gutierrez, 27 Nov. 1937, *Kalela s.n.* (S), Lago Gutierrez, *Kalela 1277* (S); Puerto Moreno (Los Juncos), San Ramón, Loma Grande, *Vellerini 265* (BAA); Puerto Moreno (Los Juncos), Ea. San Ramón, *Vellerini 257* (BAA); 6 km from Bariloche, *Pedersen s.n.* (CTES); Leleque, *Soriano 2409* (BAA); Catedral Hotel, P.N. Nahuel Huapí, *Pedersen 1468* (CTES); P.N. Nahuel Huapí, *Boelcke & Correa 5864* (BAA); picada a lo largo de Martín Grande, *Boelcke & Correa 6142* (BAA); Bariloche, arroyo Guillelmo, camino a El Bolsón, *Nicora 7478* (BAA). CHILE. **II Región:** El Rincón, just N of Paposo, along trail to old Parañas Mine, *Johnston 5539* (BAA); Antofagasta, Dpto. Taltal, vic. of Aguada de Miguel Díaz, *Johnston 5407* (SGO). **IV Región:** Ovalle, bosque de Talinay, lado sur de la desembocadura del Limarí, *Muñoz & Coronel 1232* (BAA); Limarí, Cordillera de Ovalle, Tulahuén-Leiva, *Jiles 4694* (CONC). **V Región**: Valparaíso, In sylvaticus calidis collium loco dicto La Laguna, Valparaíso, 1829, *Bertero 997* (P, BAA ex P, SGO ex P); cerro Roble above Calco, *Hutchinson 59* (SGO); Valparaíso, *Iechler 2846* (US fragm. ex P, F); Cuesta La Dormida, camino entre Quillota y Santiago, *Muñoz & Schick 1545* (SGO); Aconcagua, Petorca, carretera Panamericana, 5 km N de Longotoma, *Ricardi, Marticorena & Matthei 1829* (CONC); Quillota, Limache, Cerro Cruz, *Garaventa 2248* (CONC); Quillota, cerro La Campana, *Zoellner 13135, 18030* (CONC); Cocalán, 9 Nov. 1913, *Baeza s.n.* (CONC); Archipiélago de Juan Fernández, Oct. 1872, *F. Philippi s.n.* (SGO); Quillota, Limache, cerca del pueblo, *Garaventa 6457* (CONC); Valparaíso, Cerro La Campana, *Hutchinson 45* (US); Cerro Las Vizcachas, *Hutchinson 110* (SGO); Quebrada Verde, *Muñoz & Johnson 2524* (SGO). **Región Metropolitana:** Cuesta de Chacabuco, a 3 km de la cumbre, *Muñoz & Johnson 2583* (SGO); in hills E of Tiltil, Oct. 1958, *Bailey s.n.* (CONC); Santiago, El Canelo, *Gunckel 21997* (CONC); Santiago, Río Clarillo, Quebrada Las Tinajas, *Araya 140* (CONC); Santiago, Quebrada La Plata, *Schlegel 4065* (CONC); Santiago, Macul, *Gunckel 40532* (CONC); Santiago, *Montero 538* (CONC); Santiago, Las Vertientes, *Gunckel 44566* (CONC); Farellones, *Villagrán & Mesa 414* (SGO); Santiago, Nido de Aguilas, Peñalolén, hacia Casa de Piedra, *Muñoz & Schick 2558, 2562* (SGO). **VI Región:** Prov. Colchagua, San Fernando, cerro Echaurren, *Montero 1354* (CONC); Agua Buena, al interior de San Fernando, *Muñoz & Johnson 2635, 2630* (SGO). **VII Región:** Prov. Linares, La Veguilla, camino de Linares al Melado, *Muñoz 2709* (SGO); Cajón de Los Cipreses, *von Dessauer s.n.* (SGO); Prov. Linares, Valle Gualquivilo, Baños de Azufre, *Schlegel 3645* (CONC). **VIII Región:** Prov. Concepción, La Toma, 29 Oct. 1934, *Junge s.n.* (CONC); Concepción, Nov. 1896, *Veger s.n.* (fragm. CONC-148139 ex M); Concepción, 10 Oct. 1951, *Pfister s.n.* (CONC); Concepción, *Barros 1987* (CONC); Talcahuano, Parque Hualpén, *Carrasco 266* (CONC); San Pedro, Oct. 1943, *Pfister s.n.* (CONC); San Pedro, *Ricardi, Marticorena & Torres s.n.* (CONC); San Pedro, 12 Nov. 1944, *Pfister s.n.* (CONC); San Pedro, 10 Dec. 1946, *Pfister s.n.* (CONC); Concepción, a orillas de camino Concepción–Florida, *Matthei 174* (CONC); Concepción, Cerro Caracol, *Pfister 370* (CONC); Bío-Bío, Hacienda Las Canteras, entre Antuco y Los Angeles, *Muñoz & Johnson 2737* (SGO); Entre Antuco y Tumbunleo, *Muñoz & Johnson 2732* (SGO); La Laja, Malacura, *Muñoz & Schick 1493* (SGO); Parque Nacional Laguna del Laja, Antuco, *Finot & Baeza 1* (CONC); Camino Canteras–Antuco, 20 km antes de Antuco, *Finot & Baeza 2* (CONC); Malalcura, cerros, *Finot & Baeza 7* (CONC); Parque Nacional Laguna del Laja, Los Barros, sector Aduana, *Finot & Baeza 14* (CONC); entre Chacay y canchas de Sky, *Finot & Baeza 2074* (CONC); cercanías de Rere, Yumbel, *Muñoz 2717* (SGO); Isla Quiriquina, *Gunckel 13797* (CONC); Ñuble, camino a las Termas, 30 km de Chillán, *Muñoz & Johnson 2676* (SGO); Atacalco, 26 Nov. 1944, *Pfister s.n.* (CONC); 5 km E de Quillón, *Hutchinson 212* (SGO, F); Concepción, 1 Nov. 1927, *Barros s.n.* (CONC); Tomé, 24 Nov. 1925, *Barros s.n.* (CONC); Lirquén, 11 Dec. 1950, *Ricardi s.n.* (CONC); Tomé, 14 Nov. 1925, *Barros s.n.* (CONC). **IX Región:** Malleco, Lumaco, Santa Clara, *Gunckel 630* (CONC); Laguna Galletué, *Montero 4956* (CONC); Quechumalal, Pampa del Olvido, Mar. 1958, *Schlegel s.n.* (CONC); Valle de Lonquimay, *Pfister s.n.* (CONC); Cautín, Temuco, Cerro Ñielol, *Montero 4508* (CONC); Malleco, Parque Nacional de Nahuelbuta, Piedra del Aguila, *Ricardi, Marticorena & Matthei 1976* (CONC); Termas de Tolhuaca, *Gunckel 16027* (CONC); Prov. Cautín, Temuco, Padre Las Casas, *Montero 1962* (CONC); Cautín, Volcán Llaima, *Gunckel 15101* (CONC); Villarica, Tromén, Límite Chileno-Argentino, *Ricardi & Matthei 27* (CONC). **X Región:** Valdivia, Jan. 1860, *R. A. Philippi s.n.* (SGO); Llanquihue, Puerto Varas, Petrohué, *Marticorena, Weldt & Crisci 1982* (CONC); Río Palena, Jan. 1887, *Delfin s.n.* (SGO); Chiloé, Lago Río Negro, *Villagrán, Aguila & Leiva 6954* (CONC); Valdivia, San Juan, Jan. 1855, *R. A. Philippi s.n.* (SGO); Lago Llanquihue, without date, *Philippi s.n.* (SGO); Puerto de Corral, *Muñoz & Johnson 3211* (SGO); Puerto Montt, Feb. 1858, *Philippi s.n.* (SGO); Puerto Montt, *Fonck 71* (SGO). **XI Región:** Aisén, Cohaique, *Schlegel 2371* (CONC). **XII Región:** Tierra del Fuego, San Sebastián, *Ricardi & Matthei 236* (CONC); Caleta Josefina, *Ricardi & Matthei 166* (CONC).

8b. Trisetum caudulatum Trin. var. **correae** Nicora, Fl. Patag. 8(3): 254, fig. 164e. 1978. TYPE: Argentina. Chubut: Futaleufú, Lago Futalaufquén, *A. Soriano 4334* (holotype, BAA-3365!).

Ovary and caryopses with trichomes at the apex.

Distribution and habitat. Nicora (1978) described this variety on the basis of material collected in Neuquén, Río Negro, and Chubut, Argentina. In Chile this plant grows between Región V and Región X generally between 1000 and 2000 m. Rodulfo Amando Philippi appears to be the first to have collected this species in Región X, Chile (Finot, 2002). *Trisetum caudulatum* var. *correae* grows along the Andes and is a forage species.

Phenology. Flowering between December and March.

Additional specimens studied. ARGENTINA. **Chubut:** P.N. Los Alerces, Lago Futalafquén, entre Río Desaguadero y Arroyo del Salto, *Lahitte & Roquero 277* (BA); Lago Futalaufquén, 7 Jan. 1964, *Lahitte s.n.* (BA). **Neuquén:** Dpto. Los Lagos, 3 km W de Confluencia, *González 766* (LP); Lago Traful Sur, orilla del lago, *Rúgolo de Agrasar 233* (BAA); P.N. Nahuel Huapí, Lago Trafuel, El Mirador, *Boelcke & Hunziker 3657* (BAA); P.N. Nahuel Huapi, Campamento Rio Villegas, 29 Jan. 1941, *Pérez-Moreau s.n.* (BAA, paratype). **Río Negro:** P.N. Nuahuel Huapí, faldeos cerro Santa Elena, *Fabris & Solbrig 1171* (LP). CHILE. **V Región:** Punta Imán, Cerro Roble, *Zoellner 18196* (ZOELLNER). **IX Región:** Valle de Lonquimay, 5 Jan. 1947, *Pfister s.n.* (CONC). **X Región:** Lago Llanquihue, without date, *Philippi s.n.* (SGO); Posada del Valle, Jan. 1877, *Philippi s.n.* (SGO).

9. Trisetum dianthemum (Louis-Marie) Finot, Contr. U.S. Natl. Herb. 48: 664. 2003. Basionym: *Trisetum spicatum* var. *dianthemum* Louis-Marie, Rhodora 30: 239. 1929. TYPE: Chile. X Región: Provincia de Llanquihue, grama a orillas del Río Puelo, 1872, *F. Vidal Gormaz s.n.* (holotype, SGO-PHIL-239b!; isotypes, BAA-3358!, SGO-37069!, SGO-68170 photo!, US fragm. ex SGO-PHIL-239b & photo!, US photo ex SGO-37069!).

Perennial, caespitose; culms 18–60 cm tall, geniculate, sericeous or pilose below the panicle; nodes 1 or 2, nearly basal, glabrous. Leaf sheaths 3–4 cm long, glabrous; ligule 1–1.5 mm long, membranous, truncate to obtuse, ciliate-denticulate, dorsally glabrous; blades 5–15 cm × 1.5–2.5 mm, glabrous, smooth, scabrous or ciliate on the margins. Panicles 4–8 × 1–2 cm, somewhat lax, subspiciform, shining; rachis pubescent. Spikelets 6.5–8 mm long, 2- or 3-flowered, open at the apex; pedicels 1.5–4 mm long, scabrous; rachilla 0.9–1 mm long, pubescent, the trichomes 0.2–1 mm long; glumes longer than the florets, subequal, lanceolate, the first glume nearly as long as and slightly narrower than the second glume; keel scabrous; margins hyaline; apex aristulate; first glume 6–7.5 × 0.6–0.8 mm, 1(3)-nerved; second glume 6.5–8 × 0.8–1 mm, 3-nerved; florets (first) 5.6–6.3 × 0.5–0.7 mm, upper floret ca. 5.5 mm long; lemmas glabrous, slightly scabrous on the keel, dorsally awned; apex hyaline, 2-setulate; margins hyaline; awn 3.5–7 mm long, borne on the upper 1/3 or 1/4, divaricate, weakly twisted, scabrous; callus obtuse, with a few trichomes ca. 0.2 mm long; paleas 4.2–4.5 mm long, shorter than the lemma; apex 2-setulate, 2-nerved, the nerves scabrous; anthers ca. 0.8 mm long; lodicules ca. 0.6–0.8 mm long; apex 3-lobed; ovary glabrous. Caryopses not seen.

Distribution and habitat. Endemic to southern Chile and Argentina, where it is known only from Region X in Chile and from Chubut, Argentina, between 3 and 210 m.

Comments. Louis-Marie (1929) established the new name *Trisetum dianthemum* for the illegitimate *T. biflorum* Phil. (Philippi, 1873: 568) and simultaneously placed it in varietal rank (*T. spicatum* var. *dianthemum* (Phil.) Louis-Marie). *Trisetum dianthemum* differs from *T. spicatum* (L.) K. Richt. by having glumes longer than the florets (vs. both glumes shorter than the florets in *T. spicatum*), longer spikelets (6.5–8 mm long in *T. dianthemum* vs. 4.5–6 mm in *T. spicatum*), isomorphic glumes (vs. subequal glumes in *T. spicatum*), and panicles somewhat lax, and somewhat spiciform (vs. spiciform in *T. spicatum*).

Phenology. Flowering between December and January.

Additional specimens studied. ARGENTINA. **Chubut:** Lago Los Niños, *Nicora 9610* (SI). CHILE. **X Región:** Puerto Varas, Islote frente a Punta Guano, *Marticorena, Weldt & Crisci 1967* (CONC); Prov. Valdivia, Barra del Río Bueno, *Hollermayer 1252* (CONC, LP); Queñi, Jan. 1887, *O. Philippi s.n.* (BAA-3357 fragm. ex SGO, SGO, US photo ex SGO); Panguipulli, 14 Dec. 1927, *Hollermayer s.n.* (CONC); Panguipulli, *Hollermayer 26-a* (CONC).

10a. Trisetum longiglume Hack. var. **longiglume,** Repert. Spec. Nov. Regni Veg. 7: 319. 1909. TYPE: Argentina. Mendoza: "in monte Piedra del Burrero prope San Rafael," Jan. 1897, *E. Wilczek 571* (holotype, W not seen).

Trisetum andicola Louis-Marie, Rhodora 30: 244. 1929. *Deschampsia andicola* (Louis-Marie) Valencia, Revista Argent. Agron. 8: 129, f. 2. 1941. TYPE: Chile. Santiago: Laguna Negra, 2700–4000 m, Mar. 1873, *F. Vidal Gormaz 265* (holotype, US-556459 fragm.&

photo ex SGO-PHIL-265!; isotypes, BAA-3344 fragm.!, SGO-37123!, SGO-37124!).

Perennial, caespitose; culms 20–30 cm tall, glabrous, erect or geniculate at the base; node 1, basal. Leaf sheaths 2–6 cm long, glabrous; apex with sheath auricles; ligule 0.2–2 mm, dorsally glabrous, denticulate at the apex; blades 3.5–12 cm × 1.5–2 mm, flat, glabrous, abaxially smooth, slightly scabrous on adaxial surface and margins. Panicles 3.5–6 × 1–3 cm, subspiciform, ovoid, dense, green to pale purple, the branches ascending; rachis glabrous; pedicels ca. 3 mm long, glabrous. Spikelets ca. 9 mm long, 2- or 3-flowered; rachilla 1.5 mm long, conspicuously pubescent, the trichomes up to 4 mm long; glumes usually longer than the florets, lanceolate, isomorphic, slightly tinged with green and purple; keel mostly smooth except near apex; apex attenuate, somewhat aristulate; first glume 8.5–9.5 × 0.6–0.7 mm, 1- to 3-nerved; second glume 8.5–9.5 × 0.8–1.2 mm, 3-nerved; florets 5–6.2 mm long; lemmas lanceolate, laterally compressed, dorsally awned, glabrous, slightly keeled, 5-nerved; apex 4-aristulate, apical awns are projection of the intermediate nerves; marginal apical awns hyaline, shorter than the middle apical awns: awn 8–9.5 mm long, borne near the median, 2.5–3 mm from the apex, twisted at base; callus obtuse, with trichomes 2–3.5 mm long, about 2/3–3/4 as long as the lemma; paleas 5–5.3 mm long, shorter than the lemma, hyaline, 2-nerved, the nerves scabrous; apex bidentate; anthers (0.5–)0.8–1 mm long; lodicules 0.6–0.8 mm long, hyaline, tridentate at the apex, the teeth small, the middle tooth a little larger than the lateral teeth; ovary pubescent, with a few trichomes near apex. Caryopses 2.0–2.7 mm long, rostrate, pubescent, apex with a few short curved and shining trichomes; trichomes curved and shining; hilum short, ovate; endosperm soft.

Distribution and habitat. *Trisetum longiglume* var. *longiglume* is endemic and rare to south-central Chile (Metropolitana) and Argentina (Mendoza, Neuquén, and Chubut) between 2000 and 4000 m. This species is primarily found in Andean valleys.

Phenology. Flowering between January and March.

Comments. Louis-Marie (1929) described *Trisetum andicola* on the basis of material collected in the Cordillera de Los Andes of the Región Metropolitana in Chile. Valencia (1941) transferred the taxon to *Deschampsia*. Later Parodi (1949b) thought it should be treated again as *Trisetum*. This species shows unique characters, making it easily recognized: glumes isomorphic, longer than the spikelet, the lemmatal awn borne near the middle of the lemma, long trichomes on the callus, and, in the typical variety, trichomes at the apex of the ovary and on the caryopsis.

Additional specimens studied. ARGENTINA. **Chubut:** Mt. La Torta, Rivadavia Range, 30, *Beetle & Soriano HS-381a* (US). **Neuquén:** Dpto. Minas, Paso del Macho, *Boelcke et al. 13932* (BAA); Copahue, 3 Jan. 1930, *Hutchinson s.n.* (BAA). CHILE. **Región Metropolitana:** Cajón Las Leñas, *Arroyo et al. 94447, 94454* (CONC).

10b. Trisetum longiglume var. **glabratum** Nicora, Fl. Patagonica 3: 245, f. 158. 1978. TYPE: Argentina. Neuquén: Dpto. Lácar, Estancia Meliquina, Co. Repollo, *Z. E. Rúgolo de Agrasar & E. Agrasar 573* (holotype, BAA!).

Perennial, with short rhizomes; culms 10–38 cm tall, erect, glabrous. Leaf sheaths glabrous; ligule ca. 2 mm long, glabrous, minutely denticulate at the apex; blades stiff, flat to conduplicate, abaxially glabrous, adaxially with 10 to 12 prominent, scabrous ribs; margins scabrous; lower blades 5–6 cm × 1–2 mm; upper (flag) blade 1 cm long. Panicles few-flowered (12 to 21 spikelets), linear, narrow; rachis glabrous; pedicels scabrous. Spikelets ca 10 mm long, 2-flowered; rachilla 2–2.5 mm long, pilose, the trichomes up to 3 mm long; glumes ca. 10 mm long, as long as the spikelet, isomorphic; first glume 1- to 3-nerved; second glume 3-nerved; florets 6.5–8.6 mm long; lemmas dorsally awned, glabrous, 5-nerved, the median and marginal nerves very conspicuous toward the apex, the nerves projected as 4 short apical awns; apical awns 1–2 mm long; awns 8–11 mm long, borne near the median, geniculate and twisted; callus very pubescent, the trichomes 1/2 the length of the lemma; paleas hyaline, a little shorter than the lemma; anthers 1.3–1.7 mm long; ovary glabrous. Caryopses 3.5–4.2 mm long; hilum oval.

Distribution and habitat. *Trisetum longiglume* var. *glabratum* is endemic to Argentina (Neuquén and Chubut) (Nicora, 1978; Zuloaga et al., 1994). This species occurs in rocky soils in the high Andes.

Illustrations. Nicora (1978: 247: fig. 158A–E).

11. Trisetum macbridei Hitchc., Contr. U.S. Natl. Herb. 24(8): 359. 1927. TYPE: Peru. Huaron, collected on rocky NE slope, 4200 m, 12 June 1922, *J. F. Macbride & Featherstone 1131* (holotype, US-1161510!; isotypes, F-050168!, F-517642!, P!, S-fragm.!).

Perennial, with short rhizomes; culms 20–40 cm tall, glabrous, erect; nodes 1 or 2, basal. Leaf

sheaths pilose; apex with sheath auricles as long as ligule; ligule 1–1.5 mm long, truncate-obtuse, denticulate, ciliate, dorsally pilose; blades 2–10 cm × ca. 3 mm, long, flat to conduplicate, stiff, sparsely pilose abaxially, scabrous adaxially, ciliate on the margin; upper blade 2–3 cm long. Panicles 6–8 × ca. 1 cm, spiciform, narrow, green-purple, shining; rachis glabrous. Spikelets ca. 8 mm long, 2-flowered; pedicels distally scabrous; rachilla ca. 1.5 mm long, pubescent, the trichomes ca. 1 mm long; glumes exceeding the florets by 1/3–1/2 in length, equal to subequal, ovate; keel somewhat scabrous; apex acute, aristulate, scabrous; first glume 7.5–8 × 1.1–1.5 mm, 1-nerved; second glume 7.8–8 × 1.3–1.5 mm, 3-nerved; florets ca. 4–5.5 × 0.9 mm; lemmas glabrous, green on back, somewhat purple on margins, dorsally awned; apex 2-aristulate, the apical awns 0.4–0.5 mm long; awn borne on the upper 1/3, twisted and geniculate, a little scabrous; callus obtuse, with trichomes 0.1–1 mm long; paleas 3 mm long, 1/2–2/3 as long as the lemma, hyaline, 2-nerved, the nerves scabrous; apex erose, minutely ciliate; anthers ca. 1 mm long, ovate; lodicules 0.6–0.7 mm long, with 2 or 3 small lobes at the apex, one of the lobes larger than the other two, sometimes cleistogamous flowers with anthers ca. 0.5 mm long; ovary glabrous. Caryopsis not seen.

Distribution and habitat. *Trisetum macbridei* is an endemic and rare species found only in the Andes of Central Peru. Tovar (1993) reported *T. macbridei* from Huancavélica and Pasco, between 4200 and 4500 m. This species is found on rocky slopes.

Phenology. Flowering in June.

Comments. *Trisetum macbridei* is related to *T. spicatum* (Hitchcock, 1927), from which it differs in having both glumes conspicuously longer than the florets (vs. glumes shorter than the florets in *T. spicatum*), glumes similar in shape (vs. glumes dissimilar in *T. spicatum*), culm glabrous below the panicle (vs. culm pubescent or pilose below the panicle in *T. spicatum*), and leaves pubescent (vs. glabrous in typical *T. spicatum*). On the basis of the isomorphic glumes, equal in length and width, Louis-Marie (1928, 1929) classified this species in *Trisetum* subgenus *Isolytrum*.

Additional specimens studied. PERU. **Ancash:** Huaylas, Huascarán National Park, quebrada Alpamayo above Lago Jancarurish, *Smith, Valencia & Gonzáles 9772* (F). **Junín:** Prov. Cerro Huarón, rocky lakeshore, *Asplund 11784* (S), *11793* (S, US).

12. Trisetum mattheii Finot, sp. nov. TYPE: Chile. Región I: Tarapacá, camino de Arica al Portezuelo de Chapiquiña, km 111, 18°18′S, 69°30′W, 4100 m, 9 Feb. 1964, *C. Marticorena, O. Matthei & M. Quezada 86* (holotype, CONC-88160!). Figure 1.

Gramen caespitosum; culmi 20–36 cm alti, erecti, pilosi; vaginae inferiores pilosae, superiores glabrae; ligula hyalina, triangularis, dentato-ciliata, 1.5–2 mm longa; laminae conduplicatae, inferiores pilosae, superiores glabrae; panicula spiciformis 3–5.5 × 0.5–0.8 cm, pauciflora; spicula 2-flora, 4.5–5 mm longa; glumae inaequales, inferior angustior, 1-nervia, 3.5–4.5 × 0.5–0.6 mm, lineari-lanceolata, superior 3-nervia, ovato-lanceolata, 3.8–4.7 × 0.7–0.9 mm; lemma hirsuta, aristata ad 1/3 superiorem; arista divaricata, non torta, scabra; callus obtusus, pilosus, pilis 0.2 mm longis; palea brevior quam lemma, hialina, binervata, nervis scabris, bidentato-biaristulata ad apicem; lodiculae 0.6–0.8 mm longae, bilobulatae ad apicem, lobulis acutis; stamina 3, antheris 1.1 mm longis; ovarium apice glabro.

Perennial, caespitose; culms 20–36 cm tall, purple, pubescent below the panicle, the trichomes ca. 0.5 mm long, first antrorse, then retrorse; nodes 2, glabrous. Leaf sheaths 1–4 mm long, longer than the internodes; lower sheaths pilose, with age glabrous; culm sheaths glabrous; ligule 1.5–2 mm long, subtriangular, dentate and minutely ciliate at the apex; dorsally glabrous; blades 1–6 cm × 0.5–1 mm, conduplicate, almost filiform, somewhat stiff, scabrous on the margin and adaxial surface; lower blades pilose; upper blades glabrous. Panicles 3–5.5 × 0.5–0.8 cm, tinged with purple and yellow, spiciform, narrow, linear, few-flowered, sometimes interrupted at the base, acute at the apex; rachis densely pubescent, the trichomes ca. 0.5 mm long. Spikelets 4.5–5 mm long, 2-flowered; pedicels densely pubescent; rachilla 0.6–0.9 mm long, with stiff trichomes at the base, glabrous toward the apex; beyond upper floret rachilla with an aristiform appendix up to 0.5 mm long; glumes a little shorter than the spikelet, dissimilar; apex acute, sometimes short-awned; first glume 3.5–4.5 × 0.5–0.6 mm, linear-lanceolate, 1-nerved; second glume 3.8–4.7 × 0.7–0.9 mm, ovate-lanceolate, 3-nerved; florets 3.5–4 × 0.6–0.7 mm; lemmas green at the base, purplish toward the apex, awned dorsally, hirsute, the trichomes 0.3–0.5 mm long; apex 2-aristulate, the apical awns ca. 0.3 mm long; awn 2.5–3.5 mm long, borne on upper 1/3, 1–1.5 mm from the apex, divaricate, not twisted nor geniculate, scabrous; callus pubescent, with trichomes ca. 0.2 mm long; paleas 2.8–3 mm long, shorter than the lemma, 2-nerved; keels scabrous below; apex 2-dentate, the teeth prolonged as hyaline setae; anthers ca. 1.1 mm long; lodicules 0.6–0.8 mm long, deeply bilobed at the apex; ovary glabrous. Caryopses not seen.

Distribution and habitat. Known only from the

Figure 1. *Trisetum mattheii*. —A. Habit. —B. Sheath, ligule, and portion of the blade. —C. Spikelet. —D. Floret. —E. Rachilla and palea, dorsal view. —F. Lodicules and palea, ventral view. —G. Rachilla. —H. Lodicules. —I. Caryopsis. *Marticorena, Matthei & Quezada 86* (holotype, CONC).

type locality, in Cordillera de Los Andes, northern Chile, Region I, at 4100 m.

Phenology. Flowering in February.

Comments. *Trisetum mattheii* is allied to *T. oreophilum* Louis-Marie var. *johnstonii* Louis-Marie, and can be separated from the latter by having taller culms (20–36 cm), with linear, narrow and few-flowered panicles, glabrous sheaths and upper blades, and subtriangular ligules. *Trisetum oreophilum* var. *johnstonii* is smaller (10–20 cm tall), with densely flowered, ovate panicles, pubescent sheaths and blades, and truncate ligules.

Etymology. The specific epithet honors the Chilean agrostologist, Oscar Matthei Jensen, retired Professor at the Universidad de Concepción, Chile.

13. Trisetum nancaguense Finot, sp. nov. TYPE: Chile. Región VI: Prov. Cardenal Caro, 12 km E of Pichilemu on Hwy. toward Nancagua, 34°23′S, 71°59′W, 45 m, 15 Nov. 1990, *T. G. Lammers, C. M. Baeza y P. Peñailillo 7894* (holotype, CONC-113221!; isotype F-2183048!). Figure 2.

Gramen caespitosum, 40–75 cm altum; culmus erectus vel geniculatus, glaber, folia multo excedens; vaginae laxae, pilosae; ligula 2–3 mm longa, hialina, truncata, dentato-ciliata; laminae 4–15 cm × 2–5 mm, planae, pilosae; panicula 6.5–9 × 0.8–2 cm, contracta; spicula 5.5–8 mm longa, 2- v. 3-flora, lateraliter compressa; rhachilla 1 mm longa, dense pilosa; glumae inaequales; inferior gluma 3.5–6 × 0.2–0.4 mm, lineari-lanceolata, 1-nervata, angustior; superior gluma 5.3–7.6 × 0.7–1.1 mm, ovato-lanceolata, 3-nervata, apice acuminata; lemma hirsuta, aristata ad 1/3 superiorem; arista flexuosa vel geniculata, non torta, scabra; callus obtusus, pilosus; palea brevior quam lemma, hialina, binervata, nervis scabris, bidentato-biaristulata ad apicem; stamina 3, antheris 1.5 mm longis; lodiculae 0.8–1 mm longae, bilobulatae ad apicem, lobulis acutis; ovarium apice glabro; caryopsis 2.5–3 × 0.5–0.6 mm, glabra; endospermium liquidum.

Perennial, caespitose; culms 40–75 cm tall, glabrous; nodes 2 to 4, glabrous or pilose. Leaf sheaths shorter than the internodes, pubescent; lower sheaths 3–8 cm long; upper sheaths 15–20 cm long; ligule 2–3 mm long, truncate, dentate-ciliate; blades 4–15 cm × 2–5 mm, flat, soft, pubescent abaxially, sparsely pilose adaxially. Panicles 6.5–9 × 0.8–2 cm, subspiciform, contracted, sometimes interrupted at the base, silvery-green to weakly purple; rachis scabrous. Spikelets 5.5–8 mm long, 2- or 3-flowered; pedicels 2–3.5 mm long, pilose to scabrous; rachilla ca. 1 mm long, pilose, the trichomes 2–3 mm long; glumes dissimilar, shorter than the florets, greenish; margins membranous, margins and apex tinged with purple; first glume 3.5–6 × 0.2–0.4 mm, linear-lanceolate, subulate, 1-nerved; keel scabrous on upper half; apex acute to shortly awned, the awn up to 1 mm long; second glume 5.3–7.6 × 0.7–1.1 mm, oval-lanceolate, awned at the apex, 3-nerved; keel scabrous; florets 6.5–7.5 × 0.6–0.7 mm; lemmas dorsally awned, hirsute, green dorsally; margins and apex hyaline, tinged with purple; apex biaristulate, the awns ca. 1 mm long; awn 6–9 mm long, borne on the upper 1/3, 1.5–2.5 mm below the apex, geniculate, not twisted; paleas 4–5 mm long, shorter than the lemma, hyaline; apex biaristulate; anthers ca. 1.5 mm long, yellow; lodicules 0.8–1 mm long, apex bilobed, the lobes acute; ovary glabrous. Caryopses 2.5–3 × 0.5–0.6 mm, glabrous; endosperm liquid.

Distribution and habitat. *Trisetum nancaguense* is endemic to Chile, ranging from Región Metropolitana to VIII Región, between 33°20′S and 36°50′S and from 45 to 2450 m altitude.

Phenology. Flowering in November and February.

Comments. *Trisetum nancaguense* appears related to *T. barbinode* Trin., from which it differs in having pubescent blades (vs. glabrous), leaf sheaths shorter than the internodes (vs. longer), glumes shorter than the florets (vs. equaling or longer than the spikelet), first glume 1-nerved (vs. 1- or 3-nerved), lemma hirsute, i.e., covered with short and stiff trichomes (vs. lemmas pubescent, i.e., covered by short and softer trichomes), and by its distribution in the Central Valley (Depresión Intermedia) and coast in Central Chile at low elevations (*T. barbinode* occurs in the Cordillera de Los Andes, usually above 1000 m).

Paratypes. CHILE. **Región Metropolitana:** Cordillera, Valle Nevado, *E. Bayer 4608* (CONC). **VII Región:** Maule, Cerro al SW de Coronel de Maule, *G. L. Stebbins 9061* (SGO). **VIII Región:** Concepción, camino entre Concepción y Bulnes km 42, *Villarroel & Weldt 151* (CONC).

14a. Trisetum oreophilum Louis-Marie var. **oreophilum,** Rhodora 30: 221. 1929. TYPE: Peru. Cuzco: moist grassland, high up ravine above Olloutaytambo, 3600 m, 5 Dec. 1923, *A. S. Hitchcock 22535* (holotype, US-1164163!).

Perennial, caespitose; culms 15–60 cm tall, puberulent to densely pubescent below the inflorescence; nodes 2, glabrous. Leaf sheaths shorter than the internodes; lower sheaths pubescent; upper sheaths glabrous; ligule 2–4.5 mm long, dorsally glabrous, denticulate at the apex; blades flat, glabrous, usually with long trichomes near the base; lower blades 8–16 cm × 2 mm; upper leaf blades 3.5–5 cm long. Panicle (5–)7–11 × 0.8–1.5 cm,

Figure 2. *Trisetum nancaguense*. —A. Habit. —B. Sheath, ligule, and portion of the blade. —C. Spikelet. —D. Floret. —E. Palea, dorsal view. —F. Palea, ventral view. —G. Rachilla. —H. Lodicules. —I. Caryopsis. *Lammers, Baeza & Peñailillo 7894* (holotype, CONC).

subspiciform to spiciform, linear, narrow, densely-flowered, interrupted at the base, purplish-green, shining, rachis pubescent. Spikelets 3.5–4.5 mm long, 2- or 3-flowered, purple; pedicels pubescent; rachilla ca. 0.7 mm long, with long trichomes at the base; glumes unequal, shorter than the florets, dorsally green and purple; margins hyaline; apex acute; first glume 2.2–3.6 × 0.4–0.6 mm, narrower and usually shorter than the second glume, 1-nerved; second glume 2.8–4.1 × 0.6–0.9 mm; florets 3.5–4.6 mm long; lemmas pubescent to sparsely pubescent, dorsally awned; margins hyaline; apex 2-aristulate; callus obtuse, with short trichomes; awn 1.5–4 mm long, scabrous, borne on the upper 1/3, 1–1.5 mm below the apex, not twisted nor geniculate, curved, scabrous, sometimes with short trichomes at the base; paleas 2.8–3 mm long, shorter than the lemma, hyaline, 2-nerved, the nerves scabrous; apex 2-dentate; anthers 1–1.2 mm long, yellow; lodicules ca. 0.6 mm long; apex bilobed, hyaline; ovary glabrous. Caryopses ca. 2.5 mm long, glabrous; endosperm liquid.

Distribution and habitat. *Trisetum oreophilum* var. *oreophilum* is found in Ecuador, Peru, and Bolivia, along the Cordillera de Los Andes, between 2900 and 4600 m. This species occurs in moist grasslands and ravines.

Phenology. Flowering between November and May.

Comments. Renvoize (1998) considers *Trisetum oreophilum* a synonym of *T. spicatum*. As Louis-Marie (1928, 1929) correctly pointed out, *T. oreophilum* is a very homogeneous taxon, apparently more closely allied to *T. rosei* Scribn. & Merr. (both species share pubescent lemmas and a caespitose growth habit) than to *T. spicatum*. *Trisetum oreophilum* can be distinguished from *T. rosei* by having scabrous awns (plumose in *T. rosei*), smaller spikelets (3.5–4.5 mm long vs. 5–7 mm long in *T. rosei*), subequal glumes (unequal in *T. rosei*), and glumes and paleas with scabrous keels (vs. ciliate in *T. rosei*). *Trisetum rosei* grows in Guatemala and Mexico (Espejo-Serna et al., 2000; Finot et al., 2004).

Additional specimens studied. BOLIVIA. **La Paz:** Región Andina, *Buchtien 6468* (US); Andean Region, *Buchtien 8839* (S); vicinity of La Paz, *Mandon 1309* (CONC), *1857* (BAA); Murillo, Valle de Palca, Huasicapampa, *Asplund 1028, 2057* (S); Chijini, *Asplund 2010* (S); Challapampa, *Asplund 3798* (S); Omasuyos, Isla del Sol, Yumani, *Asplund 3585* (S); Murillo, La Paz Calacoto 18 km hacia Collana, *Beck 13788* (SI); Cerro Calvario, *Parodi 10127*; *10122* (BAA). ECUADOR. **Azuay:** P.N. Cajas, NW Cuenca along Río Miguir, *Peterson, Annable & Poston 8866* (US). **Bolívar:** Hacienda Talahua, *Penland 584 & Summers* (F). **Chimborazo:** 15.5 km SE of main square of Chambo and SE of Río Bamba on rd. to Alao, *Peterson, Judziewicz, King & Jørgensen 9176* (US); 9 km NE of San Juan de Velasco on rd. to Lago Colta, *Peterson, Judziewicz, King & Jørgensen 9239* (US); Urbina, tow. Mt. Chimborazo, *Asplund 7896* (S). **Cotopaxi:** Lag. Quilotoa, *Laegaard 101347* (QCA); P.N. Cotopaxi, Limpiopungo, *Roig J. 12000* (MERL). **Pichincha:** *Sodiro 1893* (US-1163177, paratype); N slope of Mount Corazón, *Asplund 17550* (S); San Juan, tow. Chiriboga, *Asplund 16131* (S); slope of the Pichincha above Lloa, *Asplund 7547* (F, S); Quito, Panecillo, *Asplund 6023* (F). PERU. **Ancash:** Huari, Huascarán Natl. Park, Quebrada Rima Rima, a lateral valley of Quebrada Carhuazcancha, *Smith, Valencia, González & Buddensiek 12224* (F); Huaylas, Huascarán Natl. Park, Quebrada Los Cedros, *Smith, Valencia & Minaya 9943* (F). **Cajamarca:** Celendín, Jalca de Kumulca, *Sagástegui, Mostacero & Leiva 12056* (F); Lagunas Maqui-Maqui, *Sánchez-Vega & Cabanillas 6790* (F); Hualgayoc, a 31 km de Bambamarca, arriba de la ciudad de Hualgayoc, sobre la ladera sur, *Sánchez-Vega, Molau & Ohman 3800* (F); Celendín, Quebrada de Sendamal, sobre la carretera a Celendín, *Sánchez-Vega, Molau & Ohman 3812* (F); Sexcemayo, cerro Mahoma al W de Cajamarca, *Sánchez-Vega & Castillo 6370* (F); Cajamarca-Chotén, en el arboretum de CICAFOR, a 4 km de la carretera Pacasmayo–Cajamarca, desvío la altura del km 155, *Sánchez-Vega, Torrel & Medina 2557* (F); Cajamarca, a la altura del Paso El Gavilán, *Sánchez-Vega et al. 1380* (F). **Cuzco:** north of city, *Hitchcock 22471* (US); Rodadero, *Marin 1432* (US); cerro, *Vargas 7045* (US); Urubamba, large eroded rock called Maranqaqa on Inca plaza called Capellanpampa, *Davis et al. 1381* (F). **Huancavelica:** Prov. Huancavelica, entre Huaytanayocc y Manta, *Tovar 2539* (US); Prov. Tayacaja, Hacienda Huari, *Salaverry 17* (US); Hacienda Alalay, entre Mejorada y Pampas, *Tovar 2474* (US); Prov. Castrovirreina, Choclococha, *Tovar 2933* (US). **Junín:** Río Blanco, *Swallen 7064* (US); Res. Nac. Junín, Ondores, *Pettersson 41, 57* (S); Goyllarisquisca, NW part of Junín, *Hitchcock 22323* (US-1164158, paratype); Cerro de Pasco, *Hitchcock 22254* (US-1164159, BAA-3408, paratype); La Quinhua, Cerro de Pasco, *Hitchcock 22271* (US); Oroya, *Hitchcock 22184* (US); Hacienda Atocsaico, near Junín, *Hitchcock 22199* (US).

14b. Trisetum oreophilum var. **johnstonii** Louis-Marie, Rhodora 30: 237. 1929. TYPE: Argentina. San Juan: Andes of NW San Juan, Arroyo Tambillos, 4300 m, 10 Jan. 1926, *I. M. Johnston 6097* (holotype, GH not seen; isotypes, BAA-3409!, SGO-59037!, SI fragm. ex US!, US-1297379!).

Perennial, caespitose; culms 10–20 cm tall, glabrous or pubescent below the inflorescence; node 1. Leaf sheaths pilose; upper sheath inflated, striate: ligule 0.5–1 mm long, truncate, dentate-ciliate; blades flat, pilose; lower blades 3–8 cm × 1–1.5 mm, flat to conduplicate; upper blade 1–5 cm × ca. 1 mm, conduplicate. Panicles 2–4.5 × 0.8–1.5 cm, oval, spiciform, dense, interrupted at the base, green and purple; rachis glabrous or pubescent. Spikelets 3.5–4.5 mm long, 2- or 3-flowered, subsessile or with pedicels up to 3 mm long, scabrous; rachilla ca. 1 mm long, densely pubescent, with

trichomes up to 1.5 mm long; glumes subequal, shorter than the florets or the second glume as long as the florets; keel scabrous; apex acute; first glume 2.7–4 × 0.4–0.9 mm, 1- or 3-nerved, the lateral nerves, if present, very short; second glume 3.3–4.7 × 0.5–1.2 mm, 3-nerved; florets 3.5–4 × ca. 0.7 mm; lemmas awned dorsally, purplish near the apex; apex biaristulate, pubescent; awn 2–3.5 mm long, somewhat twisted at the base, geniculate or curved, scabrous; callus obtuse, with trichomes ca. 0.5 mm long; paleas 2.2–3.5 mm long, shorter or about as long as the lemma, hyaline, 2-nerved, the nerves scabrous; apex bidentate; anthers ca. 1.1 mm long; lodicules ca. 0.5 mm long, bilobed at the apex, hyaline. Caryopses 1.6–2 × 0.3–0.5 mm, glabrous or with 4 to 6 shining curved trichomes at the apex; endosperm liquid.

Distribution and habitat. *Trisetum oreophilum* var. *johnstonii* is found in northern Chile and Argentina (27°S–33°50′S) along the Cordillera de Los Andes, between 2900 and 4600 m.

Phenology. Flowering between December and February.

Comments. Finot (2003) cited by error *Johnston 6079* instead of *Johnston 6097* as the type of *T. oreophilum* var. *johnstonii*. This species is frequently confused with *T. preslei*, from which it differs in having hairy leaves (vs. leaves glabrous in *T. preslei*), glumes shorter than the florets (vs. glumes equaling or exceeding the florets in *T. preslei*), first glume 2.7–4 mm long (vs. first glume 4.5–6 mm long in *T. preslei*), and second glume 3.3–4.7 mm long (vs. second glume (4.5–)5.5–6.5 mm in *T. preslei*).

Additional specimens studied. ARGENTINA. **Mendoza:** Dpto. San Rafael, Paso Cruz de Piedra, Refugio Perón, *Roig 50* (MERL); San Carlos, camino a Laguna Diamante, *Boelcke 4132* (BAA); San Carlos, Laguna Diamante, *Boelcke et al. 10011, 10039* (BAA); Laguna Diamante, El Paramillo, *Boelcke et al. 10061* (BAA); Luján, Lagunita del Plata, *Trombotto & Ahumada 11105* (MERL); Luján, Cordillera Frontal, Cordón del Plata, Lagunita del Plata, 22 Feb. 1984, *Trombotto s.n.* (MERL); Las Cuevas, Quebrada Benjamín Matienzo, *Pérez Moreau 144* (BA, pro parte); Cordillera del Portillo de la Llareta entre el Paso del Portillo y la Laguna del Diamante, entre Arroyo de La Cascada y Corrales Negros, *Kurtz 11086* (SI). **Neuquén:** Chos Malal, cajón inferior del Arroyo Turbio (Arroyo Domeyko), *Boelcke et al. 11318* (BAA). **San Juan:** Calingasta, entre Paso Espinacito Sur y Quebrada Honda, 12 Feb. 1950, *Pérez-Moreau & Perrone s.n.* (BA); Cordillera de Colanguil, quebrada del Salto, *Pérez-Moreau 30–258* (BA, BAA); Espinacito, Los Frías, Río Las Leñas, *Roig 11950* (BAA); alta cordillera de San Juan, Laguna Pachón, *Koptaluti & Gómez 5816* (SI); Dpto. Iglesia, Mina Fierro Nuevo, Quebrada de los Chilenos, 26 Feb. 1950, *Perrone s.n.* (BA). CHILE. **III Región:** Copiapó, Laguna del Negro Francisco, *Muñoz 3981* (SGO); Huasco, Quebrada Cantarito, entre Quebrada Marancel y Portezuelo de Cantarito, *Marticorena et al. 83462-B* (CONC); Km 42 Río del Estrecho, *Arancio, Squeo & León 94250* (CONC, USL); Quebrada Los Barriales, *Arancio, Squeo & León 94043* (USL). **IV Región:** Choapa, Cordillera de Illapel, Caletón Blanco, *Jiles 4246* (CONC); Cordillera de Combarbalá, Ha. Ramadilla, *Jiles 4801* (CONC); Cajón de Los Pelambres, *Teillier 1536* (CONC); Elqui, Cordillera Doña Ana, Quebrada del Negro, *Arancio 92129* (CONC, USL); Cordillera de Ovalle, San Miguel-Los Pingos, *Jiles 5889* (CONC); Cordillera de Ovalle, Los Pingos, *Jiles 5888* (CONC); Cordillera de Doña Ana, 23 Mar. 1994, *Arancio s.n.* (USL); Cordillera de Doña Ana, *Arancio 93021* (USL); Limarí, Cordillera de Ovalle, Punta de Huana-Río Molles, *Jiles 4136* (CONC); Doña Rosa, nacimiento de Quebrada Larga, *Jiles 2952* (CONC); Vegas San Miguel, *Jiles 3649* (CONC, SGO). **Región Metropolitana:** Santiago, Paso de las Nieves Negras, *Gunckel 20465a* (CONC); Cajón del Maipo, *Gunckel 20295* (US).

15. **Trisetum phleoides** (d'Urv.) Kunth, Revis. Gramin. 1: 101. 1829. Basionym: *Avena phleoides* d'Urv., Fl. Iles Malouin. 30(19). 1825. *Trisetum subspicatum* var. *phleoides* (d'Urv.) Hack., Svenska Exped. Magell. 3(5): 222. 1900. *Trisetum spicatum* subsp. *phleoides* (d'Urv.) Macloskie, Rep. Princeton Univ. Exp. Patagonia, Botany 8: 206. 1904. TYPE: South America. Falkland Islands [Islas Malvinas], Soledad, *d'Urville 3*: (holotype, P not found; isotypes, BAA-3411!, US-fragm. ex P!).

Trisetum hirsutum Phil., Anales Univ. Chile 46(43): 565. 1873, non (Gaudin) Schrad., Linnaea 12: 443. 1838. *Trisetum spicatum* (L.) K. Richt. var. *hirsutum* Louis-Marie, Rhodora 30: 239. 1929. TYPE: Chile, "Estrecho de Magallanes, de los alrededores de la colonia chilena," *R. A. Philippi s.n.* (holotype, SGO-PHIL-235!; isotypes, SGO-63600!, 37057!, US-81775!, US fragm. ex SGO-PHIL-235 & photo!, US photo ex SGO-37057!).

Perennial, with short rhizomes; culms 5–24 cm tall, erect, densely pilose below the panicle; trichomes 0.5–0.7 mm long, antrorse below the panicle, then retrorse below. Leaf sheaths pilose; ligule 1.5–2 mm long, truncate, ciliate, dorsally pubescent; blades flat or conduplicate, pilose, ciliate on margins near the ligule. Panicles 2–6 × 0.5–1.5 cm, spiciform, dense, green-yellowish, sometimes tinged with purple, sometimes included in the upper sheath. Spikelets ca. 6.5 mm long, 2- to 4-flowered; rachilla ca. 0.8 mm long, pubescent, the trichomes up to 2 mm long; glumes subequal, longer than the florets, rarely the first glume a little shorter than the spikelet; keels ciliate; apex short aristulate; first glume 4–6.5 × 0.5–0.6 mm, 1-nerved; second glume 5–6.5 × ca. 0.7 mm, 3-nerved; lemmas dorsally awned, glabrous; apex 2-aristulate, the awns 0.5–1 mm long; awn ca. 6 mm long, curved, not strongly twisted or geniculate,

scabrous, borne on the upper 1/3; callus with short trichomes, the trichomes ca. 0.2 mm long; florets ca. 4 mm long; paleas ca. 3.5 mm long, shorter than the lemma, 2-nerved, the nerves scabrous; apex bidentate; anthers ca. 1.2 mm long; ovary glabrous. Caryopses not seen.

Distribution and habitat. *Trisetum phleoides* is endemic to southern Argentina and Chile, occurring between 50°S and 55°S latitudes and between 15 and 1000 m.

Phenology. Flowering between November and March.

Illustrations. Nicora (1978: 247, fig. 161A–D).

Comments. *Trisetum phleoides* is perhaps related to *T. spicatum*. Both species have spiciform panicles and culms densely pilose below the inflorescence. *Trisetum phleoides* was placed as a variety or subspecies of *T. spicatum* by Macloskie (1904), Louis-Marie (1928, 1929), and Hultén (1959). Nicora (1978) accepted this taxon at the species level. It is evident from an annotation label written in 1935 by L. Parodi on the type of *Avena phleoides* at BAA that he considered *T. phleoides* a good species and closely related to *T. spicatum*: "Es una buena especie limitada a las Malvinas y Región Fueguina, afín a *T. subspicatum*." *Trisetum phleoides* differs by having pilose blades (vs. glabrous or puberulent in *T. spicatum*), dorsally pubescent ligules (vs. glabrous in *T. spicatum*), glumes that are ciliate on the keels (vs. scabrous in *T. spicatum*) and longer than the florets (vs. glumes shorter than the florets in *T. spicatum*).

Additional specimens studied. ARGENTINA. **Santa Cruz:** Río Fósiles, 1905, *Dusén s.n.* (S); Güer Aike, Estancia Las Viscachas, Pan de Azúcar, *Arroyo, Boelcke, Gómez, Moore & Romanczuk 491* (SI); Guer Aike, curso superior del Río Turbio, entre Estancia La Primavera y puesto Tres Marías, *Roig et al. 444* (SI); P.N. Perito Moreno, Río Chico, *Villamil 8396* (CONC). **Tierra del Fuego:** Ushuaia, cerro Martral, 5 Feb. 1986, *Roig J. s.n.* (MERL); Valle de Olavaia, *Alboff 1039* (SI); Río Fuego, 9 Jan. 1919, *Pico s.n.* (BAA); Ushuaia, Mar 1902, *Skottsberg s.n.* (S); Ushuaia, *Skottsberg 236* (S), Feb. 1896, *Alboff s.n.* (LP); Hito XIX, 6 Feb. 1942, *Castellanos s.n.* (BAA); alrededores de Ushuaia, *Hunziker 8200* (BAA); Ushuaia, canal Beagle, Punta Segunda, *Grondona 7340* (BAA); Isla de los Estados, Puerto Abrigado, *Castellanos 1937* (BA); Salto del Río Grande, 30 Jan. 1912, *Hicken s.n.* (CONC); Islas Malvinas, *Skottsberg 69* (S); Ushuaia, Monte Olivia, orillas del Rio Olivia, *Ferraro, Messuti & Vobis 4676* (CTES); Ushuaia, Rio Pipo, Camping Mun. Monseñor Aleman, 11 Mar. 1995, *Ferraro, Messuti & Vobis 4703* (CTES); Ushuaia, península detras del aeródromo (La Mision), *Luti 1640* (CORD); Ushuaia, cerros proximos al monte Olivia, *Luti 1426* (CORD); Ushuaia, Ruta Nacional J, Puerto Haberton, *Fortunato 4823 & Elechosa* (CORD); Ushuaia, *Pennington 450b* (SI); Turbera de Oldenbourg, *F. Roig, C. Roig & F. A. Roig 14911* (MERL); camino del bosque al salto del Río Grande, 30 Jan. 1912, *Hicken s.n.* (SI); Isla de Los Estados, Puerto Cook, Mar. 1882, *Spegazzini s.n.* (LP). CHILE. **XII Región:** Patagonia Occ., 5 Jan. 1897, *Dusén s.n.* (S); Magallanes, *Anderson 387* (S); Punta Arenas, cerros de canchas de sky, *Ricardi & Matthei 316* (CONC); cerros de canchas de sky, 120 m, *Pfister & Ricardi s.n.* (CONC); Punta Arenas, Río de las Minas, *Barrientos 224* (CONC); Tierra del Fuego, 1769, *Banks & Solander s.n.* (S); Tierra del Fuego, sector Vicuña, Lote 12, Forestal Trillium, *Pisano, Henríquez & Domínguez 7566* (CONC); Isla Navarino, *Tsujii 172* (CONC); Isla Navarino, Mont au dessus du Port Williams, Nov. 1958, *de La Rüe s.n.* (P); Fuegia Orientalis, Feb. 1879, *P. Ortega s.n.* (SGO); Prov. Tierra del Fuego, Río Hondo, *Pisano 2451* (CONC).

16. Trisetum preslei (Kunth) E. Desv., in Gay, Fl. Chil. 6: 347. 1854. Basionym: *Avena preslei* Kunth, Enum. Pl. 1: 304. 1833. TYPE: Chile. "Hab. in Cordilleris chilensibus," *T. Haenke s.n.* (holotype, PR-198805!; isotypes, BAA-3413 fragm.!, LE-TRIN-1933.02!, MO-2106485 not seen, US-81803!).

Trisetum lasiolepis E. Desv., Fl. Chil. 6: 346. 1854. Syn. nov. TYPE: Chile. *C. Gay s.n.* (holotype, P!; isotypes, BAA fragm. ex P not seen, CONC fragm. ex P!, GH not seen, P!, SGO photo ex P!, US-91366 fragm. ex P!).

Deschampsia lasiantha Phil., Linnaea 33: 290. 1864. *Trisetum preslei* var. *lasianthum* (Phil.) Louis-Marie, Rhodora 30: 238. 1929. TYPE: Chile. Andes de Hurtado, *C. Gay s.n.* (holotype, SGO-63603!; isotype, SGO-71900 photo!).

Trisetum buchtienii Hack., Z. Bot. 54: 290. 1904. *Trisetum preslei* var. *buchtienii* (Hack.) Louis-Marie, Rhodora 30: 238. 1929. TYPE: Chile. "Las Calaveras, 3200 m, Uspallata Pass, der chilenischen Hoch-Cordillere," 14 Feb. 1903, *O. Buchtien s.n.* (holotype, S!; isotypes, BAA-3361!, US-1099519!).

Perennial, caespitose; culms 3–19(–30) cm tall, erect or geniculate at the base, densely pilose or tomentose below the inflorescence, glabrous below; nodes 1 or 2. Leaf sheaths up to 6 cm long, glabrous; upper sheaths usually inflated and striate; ligule 0.5–1.5 mm long, a little longer on the upper leaves, oval, truncate, dentate-laciniate, ciliate; blades glabrous, adaxially scabrous especially toward the base; margins scabrous; lower blades 2–6 cm × 1–1.5 mm; upper blades 0.5–3 cm long. Panicles 2–7 × 0.5–1.5 cm, contracted, subspiciform or spiciform, densely-flowered, green or purple, exerted or included in the upper sheath; rachis covered by long trichomes or subglabrous; pedicels up to 2 mm long, pubescent. Spikelets 5–6 mm long, (1)2(3)-flowered; rachilla 1–1.5 mm long, with trichomes 1.5–2 mm long; glumes subequal, equaling or more frequently longer than the florets, delicate, translucid, with wide hyaline margins; keel scabrous; apex acute or aristulate; first glume 4–6

× 0.4–0.7 mm, linear-lanceolate, equaling or a little longer than the spikelet, a little narrower than the second glume, 1-nerved; second glume (4.5–) 5.5–6.6 × (0.6–)0.8–1.1 mm, usually longer than the spikelet, 3-nerved; florets 4.2–5.5 × ca. 0.7 mm; lemmas dorsally awned, green-yellowish, somewhat purplish toward the apex, dorsally pubescent, trichomes long, soft, up to 1 mm long; margins hyaline; apex 2-aristulate; awn 2.5–4.5 mm long, nearly as long as the lemma, borne on the upper 1/3, divaricate, geniculate and weakly twisted or more frequently curved not geniculate or twisted, pilose at the base, scabrous above; callus obtuse, pilose, with trichomes ca. 1 mm long; paleas 3.2–4.5 mm long, a little shorter than the lemma, 2-nerved, the nerves scabrous-ciliate; apex 2-dentate; lodicules 0.6–1 mm long; apex bilobed, one of the lobes larger; ovary glabrous. Caryopses 2.5–2.7 × ca. 0.5 mm, glabrous; endosperm dry.

Distribution and habitat. *Trisetum preslei* is endemic to Chile and Argentina. In Chile *T. preslei* is found along the Cordillera de Los Andes between 2200 and 3700 m, and in Argentina it occurs between 33°S and 42°S at 1800–4000 m.

Phenology. Flowering between December and February.

Illustrations. Nicora (1978: 262, fig. 169A–C).

Comments. A note by Desvaux (1854) accompanying the original description of *T. lasiolepis* indicates a close relationship of this species with *T. preslei*. In Desvaux's opinion *T. lasiolepis* could be considered as a variety of *T. preslei*. *Trisetum lasiolepis* was recognized as a good species by Louis-Marie (1928, 1929) and by Nicora (1978). Nicora (1978) distinguished *T. lasiolepis* from *T. preslei* as being taller (plants 20–40 cm tall in *T. lasiolepis* vs. 10–20 cm tall in *T. preslei*), culms glabrous or pilose just below the panicle (vs. retrorse tomentose in *T. preslei*), panicles somewhat loose, with rachis pubescent to almost glabrous (vs. panicle dense, with rachis densely tomentose in *T. preslei*), and keels of glumes and palea scabrous (vs. keels of glumes and palea normally ciliate in *T. preslei*). The type of *T. lasiolepis* at P has culms 20–30 cm tall, narrow subspiciform panicles 5–7 cm long and less than 1 cm wide, glabrous blades (lower blades 4–5 cm long; upper blades 1–2 cm long), 2-flowered spikelets 5–6 mm long, and glumes equaling the florets or the second glume longer than the florets (first glume 4 × 0.4 mm; second glume 6 × 0.8 mm). Since the morphological characters taken from the type of *T. lasiolepis* fall within the range given for *T. preslei*, we consider this a new synonym of the latter species.

Additional specimens studied. ARGENTINA. **Mendoza:** on road above Las Cuevas, below Cristo Redento, *H. & B. Mooney 546* (CONC); La Cumbre, Las Cuevas, Dec. 1908, *Spegazzini s.n.* (LP); Valle del Atuel, cerca Laguna Atuel, *Böcher et al. 1971* (BAA); Atuel Valley, near El Angulo, *Böcher et al. 1894* (BAA); Las Heras, entre Las Cuevas y Cristo Redentor, *Ruiz Leal 79* (MERL); Las Heras, entre Las Cuevas y Cristo Redentor, *Ruiz Leal 6625* (MERL); Las Heras, Cristo Redentor, *Martínez Carretero 1272* (MERL); San Rafael, valle del río Atuel, *Boelcke et al. 10226 1/2* (BAA); San Rafael, Antes de llegar Indígeno-Estribaciones Norte Volcán Overo-El Sosneado, *Lagiglia 2239* (LP); Agua Amarilla, Volcán Overo, El Sosneado, *Lagiglia & D'Antoni 1326* (LP); entre Puesto de Ubilla y La Manzanilla, en el arroyo Tordillo, *Kurtz 7599* (CORD); Calmucó, *Covas 101* (BAA); Malalhue, proximidades de la cresta de la Sierra Azul, *Méndez & Willoud c-320–7196* (MERL). **Neuquén:** Chos Malal, Cajón del Arroyo del Cruce, faldeo S del Domeyko, *Boelcke et al. 11285* (BAA); Lácar, Cerro Repollo, Estancia Meliquina, *Rúgolo de Agrasar & Agrasar 5846* (BAA); Minas, Lagunas Epu-Lauquén, Puesto de Gendarmería, *Boelcke et al. 11033* (BAA); Pino Hachado, *Parodi 3196* (US); Chos Malal, a 34 km de Tricao Malal camino a Mina de Azufre, *Boelcke et al. 11674* (SI). **Rio Negro:** El Bolsón, Cerro Piltriquitrón, *Cabrera et al. 23110* (LP); Parque Nacional Nahuel Huapi, Cerro López, *Boelcke 1972* (BAA). CHILE. **IV Región:** Coquimbo, Los Molles, Ovalle, *Zoellner 5859* (CONC). **V Región:** Los Andes, Laguna Castro, *Peñaloza et al. 91126, 91121* (CONC); entre Laguna Las Truchas y Laguna de la Turquesa, *Arroyo, Maldonado & Henríquez 91156, 91158* (CONC); Laguna Castro, *Peñaloza et al. 91122* (CONC); Aconcagua, Portillo, Laguna del Inca, *Sparre 1678* (S). **Región Metropolitana:** Cordillera de Santiago, Mar. 1899, *Reiche s.n.* (SGO); Parque Nacional El Morado, Cordillera de Los Andes frente a Santiago, *Teillier et al. 2548* (SGO); San José de Maipo, Cajón del Río Morales, *Saavedra & Pauchard 6* (CONC, SGO); Cordillera, Lo Valdés, Feb. 1950, *Gunckel s.n.* (CONC); Cajón del Maipo, *Gunckel 20297* (US); Cajón del Maipo, Hito Paso Internacional Maipo, *Villagrán et al. 8462* (SGO); Maipo, *Joseph 2948* (US); Prov. Santiago, Camino de Santiago a Mina La Disputada, 2 km antes de Pérez Caldera, *Marticorena & Matthei 664* (CONC); Cajón del Yeso, Termas El Plomo, *M. Muñoz et al. 3491* (SGO); Laguna Negra, *Lechler 2948* (US). **VIII Región:** Ñuble, Termas de Chillán, *Cabrera 3662* (LP), Feb. 1947, *Castillo s.n.* (CONC, US); Baños de Chillán, Jan. 1877, *F. Philippi s.n.* (SGO), Jan. 1878, *F. Philippi s.n.* (LP).

17. Trisetum pyramidatum Louis-Marie ex Finot, sp. nov. TYPE: Chile. Punta Arenas, Leña Dura, 28 Jan. 1946, *M. Barros 5706* (holotype, US-1869901!). Figure 3.

Planta perennis, rhizomatosa, 37–50 cm alta; culmi pilosi, inferiores glabri; folia glabra; laminae planae; ligula 2–3 mm longa, glabra; panicula pyramidata, 7–11 × 2–3 cm; spicula 6–6.5 mm longa, 2- v. 3-flora; glumae subaequales vel inaequales, spiculam aequantes, ad apicem aristulatae; gluma I: (5–)5.5–7.5 × 0.8–1 mm, 1-nervia; gluma II: 6.5–9 × 1.1–1.3 mm, 3-nervia, quam lemma sua minores vel excedentes; lemma ad dorsum scabra, ad terciam superiorem aristata; arista geniculata vel recurvata, scabra, 6–7 mm longa; callus brevi-pilosus; rhachilla pilosa 1 mm longa; palea quam lemma minor, binervia, ad

Figure 3. *Trisetum pyramidatum.* —A. Habit. —B. Sheath, ligule, and portion of the blade. —C. Spikelet. —D. Florets. —E. Palea, dorsal view. —F. Palea, ventral view. —G. Rachilla. —H. Lodicules. —I. Stamen. —J. Caryopsis. *Barros 5706* (holotype, US).

apicem bisetulosa; stamina 3, antheris 0.5 mm longis; lodiculae 0.8 mm longae, ad apicem bilobatae; ovarium glabrum; caryopsis 2.5 mm longa, glabra; endospermium granulosum.

Perennial, with short rhizomes; culms 37–50 cm tall, pubescent below the panicle, with trichomes first antrorse, then retrorse; nodes 2, glabrous. Leaf sheaths glabrous, pubescent when young; ligule 2–3 mm long, membranous, with rounded, dentate and ciliate margin; dorsally glabrous; blades 4–7 cm × 2–2.3 mm, flat, glabrous; lower blades 6–7 cm × 2–2.3 mm; upper blades 4–5 cm long, conduplicate toward the apex. Panicles 7–11 × 2–3 cm, contracted, pyramidal, yellowish-green and tinged with purple, bright; branches in trimerous whorls, the basal branches up to 3 mm long. Spikelets 6–6.5 mm long, 2- or 3-flowered; glumes subisomorphic or dissimilar, equaling or longer than the spikelet or at least the second glume longer than the spikelet, wide, lanceolate, adaxially purplish; margin hyaline; apex aristulate, hyaline; first glume (5–)5.5–7.5 × 0.8–1 mm, 1-nerved; second glume 6.5–9 × 1.1–1.3 mm, 3-nerved; florets 6.5–7 mm long; lemmas dorsally awned, scabrous; apex hyaline, biaristate; awn 6–7 mm long, borne on the upper 1/3, geniculate or only diversely curved, not twisted, scabrous, purplish; callus obtuse, with very short trichomes, the trichomes 0.2–0.3 mm long; rachilla ca. 1 mm long, pubescent, with trichomes ca. 1.5 mm long; paleas 4–5 mm long, shorter than the lemma, 2-setulate at the apex, 2-nerved, the nerves scabrous; anthers ca. 0.5 mm long; lodicules ca. 0.8 mm long, 2-lobed, the lobes acute; ovary glabrous. Caryopses ca. 2.5 mm long, glabrous; endosperm dry, granular.

Distribution and habitat. *Trisetum pyramidatum* is endemic to Chile and Argentina, between 40°S and 53°S at low elevations less than 200 m.

Phenology. Flowering between December and March.

Comments. *Trisetum pyramidatum* is morphologically similar to *T. phleoides*. This new species can be distinguished from *T. phleoides* by having wider, pyramidal-shaped panicles, (vs. spiciform in *T. phleoides*) and by having glabrous blades (vs. densely pubescent in *T. phleoides*).

Paratypes. ARGENTINA. **Río Negro:** Nord Patagonia, San Carlos de Bariloche, Feb. 1905, *Buchtien s.n.* (US). CHILE. **XI Región:** Aisén, Quitralco, 15 Dec. 1947, *Behn s.n.* (CONC). **XII Región:** Punta Arenas, Leña Dura, *Barros 5709* (US); Punta Arenas y Río de la Mina, 1 Mar. 1917, *Bonarelli 185* (SI); Rio Leña Dura, al sur de Punta Arenas, *Bonarelli 181* (SI); Río Tres Brazos, al sur de Punta Arenas, *Bonarelli 182* (SI).

18a. Trisetum spicatum (L.) K. Richt. var. **spicatum,** Pl. Eur. 1: 59. 1890. Basionym: *Aira spicata* L. Sp. Pl. 1: 64. 1753. *Aira subspicata* L., Syst. Nat. ed. 10. 2: 873. 1759, nom. illeg. superfl. *Avena airoides* Koeler, Descr. Gram. 298, 1802, nom. illeg. superfl. *Trisetum subspicatum* (L.) P. Beauv., Ess. Agrostogr. 88, 149, 1812, nom. illeg. superfl. *Trisetaria airoides* (Koeler) Baumg., Enum. Stirp. Transsilv. 3: 265. 1816, nom illeg. superfl. *Trisetum airoides* (Koeler) P. Beauv. ex Roem. & Schult., Syst. Veg. 2: 666. 1817, nom. illeg. superfl. *Koeleria subspicata* (L.) Reichb., Fl. Germ. Excurs. 49. 1830, nom. illeg. superfl. *Koeleria spicata* Reichb. ex Willk. & Lange, Prodr. Fl. Hispan. 1: 72. 1861, nom. inval. *Trisetaria spicata* (L) Paunero, Anales Jard. Bot. Madrid 9: 516. 1959. TYPE: Sweden. Lapland: 1732, *Linnaeus s.n.* (lectotype, LINN 85.7! designated (as holotype) by Edgar, New Zealand J. Bot. 36: 556. 1998; isotype, S!).

Trisetum albidum Sodiro, Revista Col. Nac. Vicente Rocafuerte 12: 84, 86. 1930. TYPE: Ecuador. Pichincha: crece en los potreros interandinos, Quito, Chillogallo, Cotocollao, and Pifo, *Sodiro s.n.* (holotype, not located; isotype, US-1163185 fragm.!).

Trisetum andinum Phil., Linnaea 29: 93. 1858. hom. illeg. non Benth. 1847. TYPE: Chile. In andibus prope Antuco invenit *C. Gay Herb. Chil. 210* (holotype, SGO-PHIL-241!; isotypes, SGO photo!, US fragm. ex SGO-PHIL-241! & photo!).

Trisetum spicatum subsp. *bolivianum* Hultén, Svensk Bot. Tidskr. 53: 224. 1959. TYPE: Bolivia. La Paz: Murillo, at the railway station La Cumbre, ca. 4700 m, 28 Apr. 1921, *Buchtien 8839* (holotype, S!).

Perennial, caespitose or with short rhizomes; culms 9–60 cm tall, erect, tomentose to densely pubescent below the panicle, with trichomes antrorse below the panicle, then retrorse below; nodes 1 or 2. Leaf sheaths 1–3(–6) cm long, glabrous; ligule ca. 1 mm long, finely denticulate; blades 1–5 cm × 1–1.5 mm, flat or conduplicate toward the apex, glabrous or rarely pubescent or scabrous, sometimes ciliate on margins. Panicles 2.5–7(–10) × 0.5–1.5(–2) cm, spiciform, gold-purplish to brown-purple, bright, usually interrupted at the base; rachis pubescent; pedicels pubescent. Spikelets 4.5–6 mm long, 2-flowered; rachilla 0.8–1 mm long, pubescent, the trichomes 0.5–1 mm long; glumes subequal, shorter than the florets, as long as 3/4 to 4/5 of the spikelet, subequal or the first a little shorter and narrower than the second glume; sometimes, the second glumes equal or a little longer than the florets, scabrous or less frequently ciliate on the keel; first glume 3.7–5 × 0.5–1 mm, lanceolate, 1- to 3-nerved; second glume 4.5–6 × 0.5–1.3 mm, 3-nerved; florets 3.8–5 × 0.7–0.8

mm, the second floret 4–4.5 mm long; lemmas dorsally awned, glabrous, scabrous, purplish toward the base, stramineous toward the apex; margin hyaline; apex 2-aristulate; awn 3.5–5 mm long, borne on the upper 1/3 or 1/4, geniculate or merely curved, sometimes twisted, scabrous, purple; callus obtuse, with trichomes 0.3–0.5 mm long; paleas 3–4 mm long, shorter or a little longer than the lemma, hyaline, 2-nerved, the nerves scabrous; anthers 0.5–1 mm long; lodicules ca. 0.6 mm long, hyaline; apex 2-lobed; ovary glabrous. Caryopses 2–2.8 × ca. 0.6 mm, glabrous; endosperm liquid.

Distribution and habitat. Cosmopolitan, probably native to Europe, introduced in America (Tovar, 1993). *Trisetum spicatum* has a circumpolar distribution (Hultén, 1959; Clebsch, 1960). In the Southern Hemisphere it is found in South America, Australia, and New Zealand (Clebsch, 1960). In North America it grows in Canada, United States, Greenland, and Mexico. In South America *T. spicatum* extends from Colombia to southern Chile and Argentina (5–4700 m) and reaches its southern limit in Tierra del Fuego at 55°S, where it is found in bogs associated with *Empetrum* L. (Empetraceae) and *Azorella* Lam. (Apiaceae). Pohl and Davidse (1994) reported *T. spicatum* for Guatemala, Tovar (1993) found this species in central and southern Peru along the Cordillera de Los Andes between 3900 and 4700 m, and Renvoize (1998) recorded this species for Bolivia (La Paz, Cochabamba, Oruro). In Argentina, Zuloaga et al. (1994) reported *T. spicatum* as occurring in Neuquén, Río Negro, Santa Cruz, and Tierra del Fuego.

Phenology. Flowering between October and March.

Comments. *Trisetum spicatum* has been treated as a complex including a vast number of subspecies and/or varieties (Louis-Marie, 1928, 1929; Hultén, 1959). Louis-Marie recognized 14 varieties, and most of these were not recognized as valid entities by later authors. Hultén (1959) divided the species into 22 infraspecific taxa, including 14 subspecies and 8 varieties. Based on a multivariate analysis of 33 morphological characters, Randall and Hilu (1986) could not differentiate any clear-cut forms or infraspecific taxa within *T. spicatum*. Louis-Marie (1928, 1929) transcribed the description made by Scheuchzer in 1719 and cited by Linnaeus (1753) in his diagnosis of *Aira spicata*: "The plant (17–30 cm high) is described as having glabrous, striate blades; ligule (ca. 1 mm long) obtuse; culms densely tomentose; panicles spike-like (ca. 1.5 × 0.7–1 cm), purplish, shining; spikelets (ca. 4 mm long) 2-flowered; glumes unequal (first shorter and narrower, second ca. 4 × 2 mm) glabrous; lemmas (ca. 4 mm long) awned dorsally on the upper 1/4; awn (ca. 4 mm long) reflexed; palea equal or subequal to the lemma; rachilla densely villous; anthers 0.6–1 mm long." This description corresponds well with the isotype of *Aira spicata* L., kept in Stockholm (S).

The type specimen of *Trisetum albidum* (US-1163185) has somewhat lax panicles and shorter spikelets (ca. 4 mm long) than in typical *T. spicatum* (4.5–6 mm long). The glumes are, in consequence, shorter (first glume 3–3.2 × 0.4–0.5 mm; second glume 3.6–4 × 0.8 mm). Since these measurements fall within the range of the original description given for *T. spicatum* in the last paragraph, we choose to relegate this form to synonymy, even though earlier VLF tentatively accepted *T. albidum* (Finot, 2003).

Chromosomes. $2n = 28, 42$ (Tateoka, 1978).

Illustrations. Hitchcock and Chase (1950: 290, fig. 390); Hultén (1959: 207, fig. 1); Nicora (1978: 247: 169A–D).

Additional specimens studied. ARGENTINA. **Chubut:** Lago La Berta, *Nicora 9603* (SI); Lago Vinter, *Roig et al. 14266* (SI, MERL); Lago Vinter, *Nicora 10235, 10284, 10344, 10348* (SI), *Nicora 9485* (CONC); Languineo, Lago El Guacho, *Nicora 9519* (CONC); Lago Cuatro, *Nicora 9344* (CONC); Río Corcovado, *Illin 169* (BAF); Lago La Para, *Nicora 10081* (SI); Valle Huemules, *Soriano 3184* (BAA). **Córdoba:** San Alberto, Sierra Grande, Pampa de Achala, Ea. La Trinidad, 25 Jan. 1984, *Cabido s.n.* (CORD). **Neuquén:** Los Lagos, Arroyo Pantojo, cascada Santa Ana, *Rúgolo de Agrasar 1093* (SI); Dpto. Minas, a 21 km de Las Ovejas, camino a las lagunas Epu-Lauquén, arroyo de Las Bandurrias, *Boelcke et al. 10801* (BAA); Cerro Malo, *Schajowskoy 55-a* (BA); Lago Nahuel Huapí, Paso de las Nubes, *Cabrera 5928* (LP); Pino Hachado, Puesto Gendarmeria, junto al arroyo, *Valla et al. 3065* (CTES); Andacollo, Arroyo Guaraco, *Cabrera 11143* (LP). **Río Negro:** P.N. Nahuel Huapí, paso de Las Nubes, *Boelcke & Correa 5590* (BAA); Valle del Río Alerce, *Boelcke & Correa 5631* (BAA); Cerro Tronador, Mallín Chileno, *Boelcke & Correa 5775* (BAA); Cerro Tronador, *Job 2431* (LP); Lago Frías, Feb. 1943, *Soriano s.n.* (BAA). **Santa Cruz:** *Spegazzini s.n.* (LP); Lago Viedma, 19 Feb. 1905, *Dusén s.n.* (S); Lago Frías, *Roquero 31* (BA); Cerro San Lorenzo, *Roquero 297* (BA); Sierra Colorada, *Dimitri & Correa Luna 119* (BA); P.N. Los Glaciares, Lago Argentino, Ea. Cristina, *Roquero 434* (BA); Río Chico, Dec. 1897, *Ameghino s.n.* (LP); Lago Argentino, Sierra de Buenos Aires, *Roquero 169* (BA); Lago Argentino, *James 189* (SI); La Vizchacha, *Burmeister 3* (SI); Guer Aike, Ea. Sofia, Secc. Cuadrado, 5 km S de Estancia Punta del Monte, *TBPA 3117* (SI); Ea. La Verdadera Argentina, Cerro de La Virgen, *Arroyo et al. 215* (TBPA 2260) (SI); Ea. Stag River, 10 km N del casco sobre el río de los Venados, *TBPA 3140* (SI). **Tierra del Fuego:** Isla de los Estados, Puerto San Juan, 28 Dec. 1933, *Castellanos s.n.* (BAA); Río Grande, lado camino, entre Punta Centolla y Cabo Viamonte, 25 Dec. 1970, *Panza s.n.* (BAA). BOLIVIA. **La Paz:** Nor Yungas, 8 mi. E of Pass on road to the Yungas

(Unduavi), *Peterson, Soreng & Laegaard 13173* (US); Murillo, Pass at the head of the Valle del Zongo and lower slopes of Nevado Hayna Potosi, *Solomon 13221* (SI ex MO); 2 km N of Millumi, *Lara & Parker 41J* (F). CHILE. **V Región:** Valparaíso, near summit La Campana, 10 mi. E of El Granizo, *Eyerdam 10047* (F, SGO). **Región Metropolitana:** Santiago, Quebrada El Yeso, *Araya 16* (CONC). **VII Región:** Curicó, Andes de Curicó, *Vidal 233, 234* (US, SGO). **VIII Región:** Ñuble, Termas de Chillán, *Jaffuel 1806-a* (SGO); Concepción, Tomeco, *Barros 3982* (LP); Parque Nacional Laguna del Laja, Los Barros, sector Aduana, *Finot & Baeza 12* (CONC); entre Chacay y canchas de sky, *Finot & Baeza 2071* (CONC). **IX Región:** Malleco, Fundo Solano, Los Alpes, Cordillera de Nahuelbuta, *Eyerdam 10257* (F). **X Región:** Valdivia, Volcán Quetrupillán, fundo Trafún, *Schlegel 7523* (CONC); Valdivia, Panguipulli, lago Riñihue, lado norte, *Montero 9557* (CONC); Osorno, Antillanca, *Sparre & Constance 10778* (CONC); Antillanca, *Schlegel 7322* (CONC); Llanquihue, Volcán Yates, *Werdermann 655* (SI); Cerro Vichadero, Casa Pangue, 14 Jan. 1953, *Pfister s.n.* (CONC). **XI Región:** Aysén, *Muñoz s.n.* (CONC); Puyuhuapi, Cerro Tesoro, *Schwabe 69* (CONC); Coihaique, *Barros 5719* (US); Estero Cofré, *Vogel 545* (CONC). **XII Región:** Parque Nacional Torres del Paine, Cerro Diente, *Arroyo & Squeo 860055-a* (CONC); Isla en el lago Grey, *Rúgolo de Agrasar 1176* (CONC); Magallanes, Rubens, 10 Jan. 1952, *Pfister & Ricardi s.n.* (CONC); Tierra del Fuego, Caleta Josefina, *Ricardi & Matthei 177* (CONC). COLOMBIA. **Caldas:** Cordillera Central, vertiente occidental, páramos del Nevado del Ruiz, *Cuatrecasas 9280* (F). ECUADOR. **Chimborazo:** *Fagerlind & Wibon 833* (S). **Cotopaxi:** 19 km east of Pilalo, *Peterson, Annable & Poston 8765* (US); Carchi, Hacienda La Esperanza, El Voladero, páramo El Angel, *Dávalos 27* (US). PERU. **Junín:** Reserva Nacional de Junín, Ondores, *Pettersson 15* (S).

18b. Trisetum spicatum var. **cumingii** (Nees ex Steud.) Finot, comb. nov. Basionym: *Koeleria cumingii* Nees ex Steud., Syn. Pl. Glumac. 1: 294. 1854. *Trisetum cumingii* (Nees ex Steud.) Nicora, Fl. Patagonica 3: 250. 1978. TYPE: Chile. Prope Valparaíso, 1831, *H. Cuming 460* (lectotype, designated here, BAA-3396 fragm. ex Herb. Nees at B! with illustration of spikelet).

Trisetum mollifolium Louis-Marie, Rhodora 30: 218. 1928, nom. nov. *Trisetum malacophyllum* Phil., Anales Univ. Chile 48: 566. 1873, non Steud., Syn. Pl. Glumac. 1: 229. 1854. TYPE: Chile. Tierra del Fuego: Fue igualmente hallada en la vecindad de la colonia chilena, en el Estrecho de Magallanes, *Lechler 1195* (holotype, SGO-PHIL-221!; isotypes, BAA-3398!, BAA-3399!; CONC-148141 fragm. & photo ex M!, CONC-148150 fragm. & photo ex B; S!, SGO-37056!; US-1126269!, US-868482 fragm. ex P!, US-81778 fragm. ex SGO-PHIL-221!, F-881353!).

Trisetum cumingii var. *santacrucense* Nicora, Fl. Patagonica 3: 250. 1978. TYPE: Argentina. Santa Cruz: Dpto. Lago Argentina, El Calafate, *M. N. Correa 2953* (holotype, BAB not seen, isotype, BAA-3370!).

Perennial, caespitose; culms 15–50 cm tall, erect, glabrous or with a few short appressed trichomes; upper internodes 12–28 cm long; nodes 2 or 3, glabrous or pilose. Leaf sheaths shorter or a little longer than the internodes, glabrous to sparsely pilose; ligules 1.5–3 mm long, glabrous or pilose dorsally, dentate, ciliate; blades 5.0–15 cm × 1–1.5 mm, flat or conduplicate, pilose; margins ciliate; upper blades 1–3.5 cm long. Panicles 4–10 × 0.8–2 cm, spiciform, green and purplish, usually interrupted at the base, shining; rachis glabrous or pilose; pedicels scabrous or with a few short trichomes. Spikelets 6–8 mm long, 2- or 3-flowered; rachilla 1–1.5 mm long, pilose, the trichomes 0.8–1 mm long; glumes unequal, acute or aristulate; keel scabrous-ciliate; first glume 4.5–7 × 0.2–0.6 mm, linear-lanceolate, narrow, shorter and narrower than the second glume, shorter than the florets, 1-nerved, attenuate toward the apex; second glume (5–)6–8 × 0.9–1 mm, ovate to ovate-lanceolate, longer than the florets, 3-nerved; lemmas dorsally awned, glabrous, scabrous toward the apex; apex 2-aristulate, the awns 0.5–1.5 mm long; awn 6–8 mm long, borne on the upper 1/3, twisted and geniculate to merely curved, scabrous, purple; callus obtuse, with trichomes ca. 0.7 mm long; paleas hyaline, 2-nerved; anthers ca. 1.5 mm long; lodicules ca. 1 mm long; apex bilobed; ovary glabrous. Caryopses glabrous; endosperm liquid.

Distribution and habitat. *Trisetum spicatum* var. *cumingii* is endemic to Chile and Argentina. In Argentina it is found south of the 40th parallel and in Chile it extends from 33°S (V Región) to southern 50°S, in Ultima Esperanza (XII Región) between 10 and 1100 m.

Phenology. Flowering between December and March.

Comments. The type of *Koeleria cumingii* in Berlin-Dahlem (B) was destroyed during WWII (Oberprieler, herb. B, pers. comm.). A fragment of this type was deposited in Buenos Aires (BAA), with a label indicating "Herb. Nees, Valparaíso, Chile, 1831, *Cuming*." This fragment was also annotated by Prof. Lorenzo Parodi in which he noted "inflorescencia de 10 cm de largo por 1.5 cm de ancho; hoja única plana, vaina pubescente—Berlín, 1936." Other annotations by Parodi include: "raquis y ramas pilosos; carena glabra; gluma (1)6–6.5 mm; gluma (2)7–7.7 mm; arista de la lemma 6–7 mm de longitud; lemma aspera?, escabriuscula." This taxon was accepted as a species by Nicora (1978), who comments that the acute glumes are longer than 4 mm and the second glumes are longer than the contiguous florets. We were able to study a large number of specimens of *T. spicatum* from South America, many of which showed the

characters commonly used to separate *T. cumingii* from *T. spicatum*, specifically the second glume longer than the contiguous floret. Nicora (1978) commented that many specimens collected in Lago Belgrano showed intermediate characteristics between *T. spicatum* and *T. cumingii*. Since there are intermediate specimens, we propose to recognize *T. cumingii* as a variety of *T. spicatum*.

Additional specimens studied. ARGENTINA. **Chubut:** Dpto. Paso de Indios, desvío a 35 km SW Ruta 24, Sa de la Butrera, Estancia La Altura, Corral de Piedra, *Arroyo, Mon & Romanczuk 200* (CONC); Lago Puelo, Estancia La Esperanza, picada al S del lago Esperanza, *Cusato & Rossow 4524* (BAF). **Neuquén:** Dpto. Los Lagos, Pto. Manzano, Lago Nahuel Huapi, *Rúgolo de Agrasar 1252* (CONC); P.N. Nahuel Huapí, entre Puerto Blest y Lago Frías, *Dimitri & Correa 176* (BA); Quetrihué, *Diem 458* (BAA). **Río Negro:** Cordón Serrucho, El Bolsón, *Roig Juñent 13353* (MERL); Lago Fonk, 21 Jan. 1942, *Pérez-Moreau s.n.* (BA); Bariloche, Puerto Blest, Nahuel Huapi, *Villamil et al. 2844* (CONC); Bariloche, cerca Río Ñirihuau, *Parodi 15582* (BAA); Río Negro, Bariloche, cerca Río Ñirihuau, *Parodi 15560* (BAA). **Santa Cruz:** Güer Aike, Río Turbio, *Roig et al. 14748* (MERL); Valle Superior del Río Turbio, faldeo de la Cordillera Chica, *Méndez & Ambrosetti* s.n. (MERL); Cordillera Chica, Cerro Punta Alta, *Ambrosetti & Méndez 29884* (MERL); Valle Superior del Río Turbio, Meseta Latorre, *Ambrosetti & Méndez 29889* (MERL); Valle Superior del Río Turbio, puesto Tres Marías, *Ambrosetti & Méndez 407* (SI); Valle Superior del Río Turbio, entre Pto. 16 La Primavera y Pto. 3 Marián, *Ambrosetti & Méndez 29874* (MERL); Cordillera Chica, *Ambrosetti & Méndez 29885* (TBPA) (MERL); Estancia Stag River, faldeos Meseta Latorre, *Ambrosetti & Méndez 27457* (MERL); Bañado 28 de Noviembre, *Ambrosetti & Méndez 29882* (MERL); Valle Superior del Río Turbio, *Ambrosetti & Méndez 29876* (MERL); Lago Argentino, *James 247* (SI); Lago Argentino, Sierra Buenos Aires, *Roquero 132* (BA); P.N. Perito Moreno, Lago Burmeister, *Rumboll 120* (BA); Ea. La Carlota, sección San Elías, *Roig, Anchorena, Méndez & Ambrosetti 115* (SI); Estancia Las Viscachas, Cerro Las Viscachas, *TBPA 2404* (CONC); Cañadón Quitapenas, *Correa 4016* (CTES). **Tierra del Fuego:** Moat, *Roig 15589* (MERL), *Roig et al. 14912* (MERL); cerca Cerro Mesa, 31 Jan. 1942, *Castellanos s.n.* (BA); Ushuaia, *A. Roig & F. Roig 14980* (MERL, BAA); Río Grande, *Castellanos s.n.* (BAA); Lago Fagnano, Monte Huehuepen, *Moore & Goodall 398* (CONC). CHILE. **VIII Región:** Lirquén, alto del camino a Tomé, *Pfister s.n.* (CONC). **X Región:** Chiloé, Isla Guafo, trayecto desde Caleta Samuel al Faro, *Villagrán & Leiva 7525* (CONC). **XII Región:** Magallanes, 15 km south of Punta Arenas, *Eyerdam, Beetle & Grondona 24133* (US); Punta Arenas, Magallanes 1864/65, *Philippi s.n.* (SGO); Cerro Castillo, *Magens 3197* (CONC); Tierra del Fuego, Ea. Cameron, *Ricardi & Matthei 184* (CONC); Tierra del Fuego, Santa Catalina, *Ricardi & Matthei 263* (CONC); Laguna Blanca, *Riggi 27/1052* (BA); Morro Chico, *Magens 3032* (CONC); Última Esperanza, *Arroyo et al. s.n.* (CONC 92112); Última Esperanza, Sierra de Los Baguales, Cerro Santa Lucía, *Arroyo s.n.* (CONC 85168); Sierra de Los Baguales, Cerro Santa Lucía, *Arroyo s. n.* (CONC 85159); Cordillera del Paine, *von Bohlen & Cavieres s.n.* (CONC 92312); Cerro Donoso, Sector Río de Las Chinas, *Arroyo, Veloso & Peñaloza 870266* (CONC); Las Cumbres, Baguales, *Ricardi & Matthei 385* (CONC); Península Muñoz Gamero, entrada al lago, *Dollenz 11* (CONC); Sector Vicuña, Lote 12, Forestal Trillium, *Pisano, Henríquez & Domínguez 7436* (CONC); Manantiales, *Magens 3428, 3433* (CONC); P.N. Torres del Paine, Río Grey, *Dollenz 1393* (CONC); Lazo, cerca Lago Toro, potrero El Chingue, *Muñoz 4104, 4144* (SGO); Magallanes, *F. Philippi s.n.* (SGO).

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Appendix 1. Alphabetical index of accepted species and varieties. Number in parentheses corresponds to the number of the species in the taxonomic treatment.

Trisetum ambiguum Rúgolo de Agrasar & Nicora (5)
Trisetum andinum Benth. (6)
Trisetum barbinode Trin. (7)
Trisetum barbinode Trin. var. *barbinode* (7a)
Trisetum barbinode var. *hirtiflorum* (Hack.) Louis-Marie (7b)
Trisetum barbinode var. *sclerophyllum* (Hack.) Finot (7c)
Trisetum caudulatum Trin. (8)
Trisetum caudulatum Trin. var. *caudulatum* (8a)
Trisetum caudulatum Trin. var. *correae* Nicora (8b)
Trisetum cernuum Trin. (1)
Trisetum dianthemum (Louis-Marie) Finot (9)
Trisetum flavescens (L.) P. Beauv. (2)
Trisetum foliosum Swallen (3)
Trisetum irazuense (Kuntze) Hitchc. (4)
Trisetum longiglume Hack. (10)
Trisetum longiglume var. *glabratum* Nicora (10b)
Trisetum longiglume Hack. var. *longiglume* (10a)
Trisetum macbridei Hitchc. (11)
Trisetum mattheii Finot (12)
Trisetum nancaguense Finot (13)
Trisetum oreophilum Louis-Marie (14)

Trisetum oreophilum var. *johnstonii* Louis-Marie (14b)
Trisetum oreophilum Louis-Marie var. *oreophilum* (14a)
Trisetum phleoides (d'Urv.) Kunth (15)
Trisetum preslei (Kunth) E. Desv. (16)
Trisetum pyramidatum Louis-Marie ex Finot (17)
Trisetum spicatum (L.) K. Richt. (18)
Trisetum spicatum var. *cumingii* (Nees ex Steud.) Finot (18b)
Trisetum spicatum (L.) K. Richt. var. *spicatum* (18a)

APPENDIX 2. INDEX TO SPECIMENS EXAMINED. NUMBER IN PARENTHESES CORRESPONDS TO NUMBER OF THE SPECIES IN THE TAXONOMIC TREATMENT AS INDICATED IN THE ALPHABETICAL INDEX (SEE APPENDIX 1).

Alboff 1039 (15), s.n. 7 Mar. 1896 (1), s.n. Feb. 1896 (15); Ambrosetti & Méndez 407 (18b), 27457 (18b), 29874 (18b), 29875 (5), 29876 (18b), 29882 (18b), 29883 (5), 29884 (18b), 29885 (18b), 29889 (18b); Ameghino s.n. Dec. 1897 (18a); Anderson 387 (15); André 3907 (6); Anonymous 10 Feb. 1955 (16); Arancio 92129 (14b), 93021 (14b), s.n. 23 Mar. 1994 (14b); Arancio, Squeo & León 94043 (14b), 94250 (14b); Araya 16 (18a), 140 (8a); Arroyo 85159 (18b), 85160 (5), 85168 (18b); Arroyo et al. 215 (18a), 9276 (5), 92112 (5), 94454 (10a), 94477 (10a); Arroyo & Squeo 860055-a (18a); Arroyo, Boelcke, Gómez, Moore & Romanczuk 491 (15); Arroyo, Maldonado & Henríquez 91156 (16), 91158 (16); Arroyo, Mon & Romanczuk 200 (18b); Arroyo, Veloso & Peñaloza 870266 (18b); Arroyo, von Bohlen, García & Gigoux 92112 (18b); Asplund 1028 (14a), 2010 (14a), 2057 (14a), 3585 (14a), 3798 (14a), 6023 (14a), 6156 (4), 6733 (4), 7215 (4), 7401 (6), 7441 (4), 7499 (6), 7547 (14a), 7896 (14a), 7978 (4), 8280 (4), 9686 (4), 11784 (11), 11793 (11), 16093 (4), 16131 (14a), 16868 (4), 17550 (14a).

Baeza s.n. 9 Nov. 1913 (8a); Bailey s.n. Oct. 1958 (8a); Banks & Solander s.n. 1769 (15); Barrientos 224 (15); Barros 1987 (8a), 3982 (18a), 5706 (17), 5709 (17), 5719 (18a), s.n. 14 Nov. 1925 (8a), s.n. 24 Nov. 1925 (8a), s.n. 1 Nov. 1927 (8a); Bayer 4608 (13); Beck 13788 (14a); Beetle & Soriano HS-381a (10a); Behn s.n. 15 Dec. 1947 (17); Benoist 2389 (6), 4389 (6); Bertero 53 (8a), 996 (8a), 997 (8a), 998 (8a.); Böcher et al. 1894 (16), 1971 (16); Boelcke 1972 (16), 4132 (14b), 10764 (7a); Boelcke & Correa 5590 (18a), 5631 (18a), 5775 (18a), 5864 (8a), 6142 (8a), 6959 (7c), 6964 (7c); Boelcke & Hunziker 3657 (8b); Boelcke et al. 9778 (7c), 10011 (14b), 10039 (14b), 10061 (14b), 10927 (7a), 11033 (16), 11285 (16), 11318 (14b), 11452 1/2 (7a), 11674 (16), 13932 (10a), 14083 (7c); Boelcke, Bacigalupo, Correa 10226 1/2 (16); Boelcke, Correa, Bacigalupo et al. 10801 (18a); Bohlen & Cavieres 92312 (18b); Bonarelli 181 (17), 182 (17), 185 (17), s.n. 1 Mar. 1917 (5); Bridarolli 2147 (8a); Buchtien 6468 (14a), 8839 (14a), 8839 (18a), s.n. 14 Feb. 1903 (16), s.n. Feb. 1905 (17); Burkart 19905 (8a), 27451 (7a); Burkart & Tamayo 16733 (4); Burkart et al. 13930 (7c); Burmeister 3 (18a).

Cabido s.n. 25 Jan. 1984 (18a); Cabrera 3662 (16), 5928 (18a), 11143 (18a), 11511 (1), 19754 (7c); Cabrera & Crisci 19145 (7c); Cabrera et al. 23024 (7c), 23170 (7c); Calderón & Rúgolo 57 (7c), 72 (7c); Cañulaf s.n. 29 Dec. 1946 (7a); Carrasco 266 (8a); Castellanos 1937 (15), s.n. 10 Feb. 1932 (1), s.n. 12 Jan. 1933 (18b), s.n. 28 Dec. 1933 (18a), s.n. 30 Jan. 1942 (5), s.n. 31 Jan. 1942 (18b), s.n. 31 Jan. 1942 (5), s.n. 6 Feb. 1942 (15); Castillo s.n. Feb. 1947 (16); Cazalet & Pennington 5740 (6); Correa 2953 (18b); Correa 4016 (18b); Correa et al. 5647 (7c); Corte 34 (8a); Covas 101 (16); Cuatrecasas 9280 (18a), 20680 (4), 20847 (4); Cuming s.n. (18b); Cusato & Rossow 4524 (18b).

Dávalos 20 (4), 27 (18a); Davidse 3226 (3); Davies s.n. 17 Feb 1938 (15); Davis et al. 1381 (14a); Dawson 1285 (8a); Dawson & Schwabe 2481 (8a); Delfin s.n. Jan. 1887 (8a); Dessauer s.n. (8a); Diehl & Bravo 10843 (7a); Diem 458 (18b), 463 (2), 3229 (7c); Dimitri & Correa 176 (18b); Dimitri & Correa Luna 119 (18a); Dollenz 11 (18b), 1393 (18b); Dusén s.n. 5 Jan. 1897 (15), s.n. 19 Feb. 1905 (18a), s.n. Apr. 1937 (15); d'Urville 3 (15).

Ehrenburg 49 (6), 137 (6); Eschscholtz s.n. (1); Eskuche & Klein 316 (8a), 1417-27 (8a), 1520-7 (7a); Eyerdam 10047 (18a), 10257 (18a); Eyerdam, Beetle & Grondona 24133 (18b).

Fabris & Crisci 7608 (7a); Fabris & Solbrig 1171 (8b); Fagerlind & Wibon 833 (18a); Ferraro, Messuti & Vobis 4676 (15), 4703 (15); Finot & Baeza 1 (8a), 2 (8a), 7 (8a), 12 (18a), 14 (8a), 2069 (7a), 2070 (7a), 2071 (18a), 2073 (7a), 2074 (8a); Fonck 71 (8a); Fortunato 4823 & Elechosa (15).

Gallinal, Aragone, Bergalli, Campal & Rosengurtt 5594 (2); Garaventa 2248 (8a), 4681 (7a), 6457 (8a); Gay 147 (8a), Gay 210 (18a), Gay s.n. (16), Gay s.n. (8a); Giaiotti et al. 23110 (16); Godoy 119 (1); Godoy, Hildebrand-Vögel & Vögel 3 (1); González 766 (8b); Grondona 5695 (1), 7340 (15); Gunckel 630 (8a), 12426 (7a), 13797 (8a), 15101 (8a), 16027 (8a), 20295 (14b), 20297 (16), 20465a (14b), 21997 (8a), 40532 (8a), 44566 (8a), s.n. Feb. 1950 (16).

Haenke s.n. (16); Harling 4537 (6); Hartweg 1449 (6); Hauman s.n. Feb. 1920 (7c); Hicken s.n. 30 Jan. 1912 (15), s.n. 30 Jan. 1912 (15); Hildebrand-Vogel 31 (1), 45 (1); Hitchcock 21059 (6), 22184 (14a), 22199 (14a), 22254 (14a), 22271 (14a), 22323 (14a), 22471 (14a), 22535 (14a); Holmgren 553 (6); Holm-Nielsen et al. 5553 (4); Hollermayer 26-a (9), 1252 (9), s.n. 14 Dec. 1927 (9); Hosseus 559 (7c), 560 (7c); Hunziker 8200 (15); Hutchinson 45 (8a), 59 (8a), 110 (8a), 212 (8a), s.n. 3 Jan. 1930, (10a).

Illin 148 (7c), 169 (18a), s.n 1 Mar. 1900 (8a), s.n. 1901 (8a).

Jaffuel 1806-a (18a), 1806-b (7a); James 189 (18a), 247 (18b); Jameson s.n. (6); Jiles 2952 (14b), 3649 (14b), 4136 (14b), 4246 (14b), 4694 (8a), 4801 (14b), 5888 (14b), 5889 (14b); Job 2431 (18a); Johnston 5407 (8a), 5539 (8a), 6097 (14b); Joseph 2948 (16); Junge s.n. 29 Oct. 1934 (8a).

Kalela 1277 (8a), s.n. 27 Nov. 1937 (8a), s.n. 28 Dec. 1937 (8a); King s.n. 1826 (1); Koptaluti & Gómez 5816 (14b); Krapovickas 3933 (8a); Kurtz 7599 (16), 11086 (14b).

Laegaard 101347 (14a), 101414 (4), 101604 (6); Laegaard et al. 103031 (4); Laegaard, Romoleroux & León 102731 (6); Lagiglia 2239 (16); Lagiglia & D'Antoni 1326 (16); Lahitte s.n. 7 Jan. 1964 (8b); Lahitte & Roquero 277 (8b), 363 (8a); Lahitte, Roquero & López 67 (8a), 486 (8a); Lammers, Baeza & Peñailillo 7894 (13); Landero 790 (5); Lara & Parker 41J (18a); Lechenby s.n. 31 May 1900 (2); Lechler 311 (8a), 1195 (18b), 1283 (1), 2846 (8a), 2948 (16); León & Calderón 1285 (8a), s.n. (7c), s.n. 17 Feb 1961 (8a); Lindig 1862 (4); Linnaeus s.n. (18a); Little & Paredes 6832 1/2 (6); Luti 1426 (15), 1640 (15).

Macbride & Featherstone 1131 (11); Magens 3032 (18b), 3197 (18b), 3428 (18b), 3433 (18b); Mandon 1309 (14a), 1857 (14a); Marin 1432 (14a); Marticorena & Matthei 664 (16); Marticorena et al. 83462-B (14b); Martico-

rena, Matthei & Quezada 86 (12); Marticorena, Weldt & Crisci 1967 (9), 1982 (8a); Martínez Carretero 1272 (16); Matthei & Bustos 111 (1); Matthei 174 (8a); Méndez & Ambrosetti s.n. 5 Feb. 1978 (18b); Méndez & Willoud c-320-7196 (16); Molau & Eriksen 3297 (6); Montero 538 (8a), 1354 (8a), 1962 (8a), 4487 (7a), 4497 (7a), 4508 (8a), 4956 (8a), 9557 (18a); Mooney, H. & B. Mooney 546 (16); Moore 848 (15); Moore & Goodall 398 (18b); Muñoz 2709 (8a), 2717 (8a), 3981 (14b), 4104 (18b), 4144 (18b), s.n. (18a); Muñoz, M. et al. 3491 (16); Muñoz & Coronel 1232 (8a); Muñoz & Johnson 2524 (8a), 2583 (8a), 2630 (8a), 2635 (8a), 2676 (8a), 2732 (8a), 2737 (8a), 3211 (8a); Muñoz & Schick 1493 (8a), 1545 (8a), 2558 (8a), 2562 (8a).

Neger s.n. Nov. 1896 (8a); Nicora 7432 (7c), 7478 (8a), 9344 (18a), 9485 (18a), 9519 (18a), 9603 (18a), 9610 (9), 10081 (18a), 10235 (18a), 10284 (18a), 10344 (18a), 10348 (18a), Nowak & Marcillo 79 (6).

Offermann s.n. 18 Jan. 1930 (8a); Ortega s.n. Feb. 1879 (15).

Paci 15731 (7c); Panza s.n. 25 Dec. 1970 (18a); Parodi 2700 (7c), 3196 (16), 10122 (14a), 10127 (14a), 11827 (1), 15321 (7c), 15560 (18b), 15582 (18b), 15611 (8a); Pedersen 1468 (8a), 1523 (1), s.n. 6 Feb. 1952 (8a); Penland 584 & Summers (14a); Pennington 450b (15); Peñaloza, Claros, Cavieres & Flores 91121 (16), 91122 (16), 91126 (16); Pérez Moreau 144 (14b, pro parte), 1949 (1), 30-258 (14b), s.n. 29 Jan. 1941 (8b), s.n. 21 Jan. 1942 (18b), s.n. 14 Jan. 1949 (8a), s.n. 1949 (7c); Pérez Moreau & Guarreva s.n. 2 Feb. 1948 (1); Pérez-Moreau & Perrone s.n. 12 Feb. 1950 (14b); Perrone s.n. 26 Feb. 1950 (14b); Peterson & Refulio-Rodríguez 15135 (4); Peterson et al. 9146 (4); Peterson, Annable & Poston 8765 (18a), 8866 (14a); Peterson, Judziewicz & King 9075 (6); Peterson, Judziewicz, King & Jørgensen 9176 (14a); 9239 (14a); Peterson, Soreng & Laegaard 13173 (18a); Pettersson 15 (18a), 41 (14a), 57 (14a); Pfister 370 (8a); s.n. (18b), s.n. 20 Oct.1943 (8a), s.n. 12 Nov. 1944 (8a), s.n. 26 Nov. 1944 (8a), s.n. 17 Jan. 1945 (7b), s.n. 10 Dec. 1946 (8a), s.n. 5 Jan. 1947 (8a), s.n. 5 Jan. 1947 (8b), s.n. 10 Jan. 1947 (7a), s.n. 12 Jan. 1947 (7a), s.n. 1 Jan. 1948 (7a), s.n. 9 Jan. 1949 (7a), s.n. 10 Oct. 1951 (8a), s.n. 14 Jan. 1953 (18a); Pfister & Ricardi s.n. 31 Dec. 1951 (15), s.n. 10 Jan. 1952 (18a); Philippi 218 (7a), 229 (7a), s.n. SGO-PHIL 220 (8a), s.n. SGO-PHIL-235 (15), s.n. Jan. 1855 (8a), s.n. Feb. 1858 (8a), s.n. Jan. 1860 (8a), s.n. Nov. 1861 (8a), s.n. 1864/65 (18b), s.n. Jan. 1877 (8b), s.n. SGO (8a), s.n. SGO (8b); Philippi, F. s.n. (18b), s.n. Oct. 1872 (8a), s.n. Jan. 1877 (7a), s.n. Jan. 1877 (16), s.n. Jan. 1878 (16); Philippi, O. s.n. Jan. 1887 (9); Pico s.n. 9 Jan. 1919 (15); Pisano 2451 (15); Pisano, Henríquez & Domínguez 6941 (15), 6962 (15), 7396 (15), 7436 (18b), 7463 (18b), 7543 (15), 7566 (15); Pittier 1435 (4); Poeppig s.n. 1828 (7), s.n. BAA 3364 (8a).

Ragonese 234 (7a); Reiche s.n. (7b), s.n. Mar. 1899 (16); Remy s.n., Oct. 1856 (6); Ricardi 5604 (7a), s.n. 11 Dec. 1950 (8a); Ricardi & Marticorena 5723/1884 (7a), 5812/1973 (7a); Ricardi & Matthei 3 (7a), 15 (7a), 27 (8a), 166 (8a), 177 (18a), 184 (18b), 236 (8a), 263 (18b), 316 (15), 335 (1), 385 (18b); Ricardi, Marticorena & Matthei 1829 (8a), 1976 (8a); Ricardi, Marticorena & Torres s.n. 2 Nov. 1957 (8a); Riggi 27/1052 (18b); Robinson & Beltran 3041 (4); Roig 1 (7c), 50 (14b), 11950 (14b), 12356 (6), 15589 (18b); Roig et al. 103 (5); Roig et al. 444 (15); Roig J. 12000 (14a), s.n. 5 Feb. 1986 (15); Roig Juñent 13353 (18b), Roig Juñent, F., C. Roig Juñent & F. A. Roig 14912 (18b); Roig, A. & F. Roig 14980 (18b); Roig, Anchorena, Méndez & Ambrosetti 115 (18b); Roig, F., C. Roig & F. A. Roig 14911 (15); Roig, Roig Juñent & Martínez Carretero 14266 (18a); 14748 (18b); Roquero 31 (18a), 132 (18b), 169 (18a), 297 (18a), 326 (8a), 434 (18a), 452 (8a); Rüe s.n. Nov 1958 (15); Rúgolo 1188 (8a), 1283 (8a); Rúgolo & Agrasar 315 (7c), 318 (7c), 570 (7c); Rúgolo de Agrasar 233 (8b), 451 (7a), 1093 (18a), 1176 (18a), 1234-1 (7a), 1234-2 (7c), 1252 (18b); Rúgolo de Agrasar & Agrasar 148 (7a), 573 (10b), 5846 (16); Rúgolo de Agrasar et al. 12381 (1); Ruiz Leal 79 (16), 3616 (7c), 6625 (16), 16886 (7c); Ruiz Leal & Roig 15023 (1); Rumboll 120 (18b).

Saavedra & Pauchard 6 (16); Sagástegui, Mostacero & Leiva 12056 (14a); Salaverry 17 (14a); Sánchez-Vega et al. 1380 (14a); Sánchez-Vega, Torrel, & Medina 2557 (14a), Sánchez-Vega, Molau & Ohman 3800 (14a), 3812 (14a); Sánchez-Vega & Castillo 6370 (14a); Sánchez-Vega & Cabanillas 6790 (14a); Schajowski 55-a (18a), 86 (7c), 133 (7c), 134 (7c), 178 (7c); Schlegel 2371 (8a), 3475 (7a), 3537 (7a), 3645 (8a), 4065 (8a), 7187 (1), 7194 (1), 7322 (18a), 7523 (18a), 8070 (1), 8122 (1), s.n. Mar. 1958 (8a); Schwabe 69 (18a); Schwing s.n. 23 Jun. 1932 (2); Sklenar & Kosteckova 80-12 (6), 812 (6); Skottsberg 69 (15), 236 (15), s.n. Mar 1902 (15); Smith, Valencia & Gonzáles 9772 (11); Smith, Valencia & Minaya 9943 (14a); Smith, Valencia, González & Buddensiek 12224 (14a); Sneidern 3027 (4); Sodiro 1893 (14a), Sodiro s.n. (18a), s.n. Oct. 1891 (4); Solomon 13221 (18a); Soriano 2409 (8a), 2490 (8a), 3184 (18a), 4334 (8b), 4352 (7c), 4847 (5), s.n. Feb. 1943 (18a); Sparre 1678 (16), 4873 (7a); Sparre & Constance 10778 (18a); Spegazzini s.n. (18a), s.n. Mar. 1882 (15), s.n. Dec. 1908 (16); Stebbins 9061 (13); Steyermark 57482 (3), 62083 (4), 62488 (4); Swallen 7064 (14a).

T.B.P.A. 2404 (18b), 3117 (18a), 3119 (5), 3140 (18a); Teillier 1536 (14b); Teillier et al. 2548 (16); Tovar 2474 (14a), 2539 (14a), 2933 (14a); Trombotto s.n. 19–22 Feb. 1984 (14b); Trombotto & Ahumada 11105 (14b); Tsujii 172 (15).

Valla et al. 3065 (18a); Vargas 7045 (14a); Vellerini 257 (8a), 265 (8a), 297 (8a); Vidal 233 (18a), 234 (18a); Vidal Gormaz 265 (10a), s.n. SGO 37066 (8a), s.n. SGO-PHIL-239b (9); Villagrán & Leiva 7525 (18b); Villagrán & Mesa 414 (8a); Villagrán et al. 8462 (16); Villagrán, Aguila & Leiva 6954 (8a); Villamil 6 (7a), 8396 (15); Villamil et al. 2844 (18b); Villarroel & Weldt 151 (13); Virlet 1382 (4); Vogel 5 (1), 519 (1), 540 (1), 545 (18a), s.n. (1).

Werdermann 655 (18a).

Zoellner 5859 (16), 13135 (8a), 18030 (8a), 18196 (8b), s.n. 2 Feb. 1968 (7a), s.n. 14 Feb. 1992 (7a).

Appendix 3. Lectotypifications of subgeneric taxa.

Trisetum sect. **Anaulacoa** Louis-Marie, Rhodora 30(359): 211, 212. 1928. TYPE: *Trisetum flavescens* (L.) P. Beauv., lectotype, designated here.

Trisetum sect. **Aulacoa** Louis-Marie, Rhodora 30(359): 211. 1928; 30(360): 243. 1929. TYPE: *Trisetum floribundum* Pilg., lectotype, designated here.

Trisetum subg. **Heterolytrum** Louis-Marie, Rhodora 30(359): 211, 212. 1928. TYPE: *Trisetum flavescens* (L.) P. Beauv., lectotype, designated here.

Trisetum subg. **Isolytrum** Louis-Marie, Rhodora 30(259): 211. 1928; 30(360): 244. 1929. TYPE: *Trisetum longiglume* Hack., lectotype, designated here.

Trisetum subsect. **Koeleriformia** Louis-Marie, Rhodora 30(359): 211. 1928; 30(360): 241. 1929. TYPE:

Trisetum micratherum E. Desv., lectotype, designated here.

Trisetum subsect. **Sphenopholidea** Louis-Marie, Rhodora 30(259): 211. 1928; 30(360): 240. 1929. TYPE: *Trisetum interruptum* Buckl., lectotype, designated here.

APPENDIX 4. LIST OF NAMES AND SYNONYMS OF ALL TAXA MENTIONED IN THIS MANUSCRIPT.

Accepted names are presented in bold and synonyms are *italicized.*

Acrospelion Besser ex Schult. & Schult. f. = **Trisetum**
Aira spicata L. = **Trisetum spicatum** var. **spicatum**
Aira subspicata L. = **Trisetum spicatum** var. **spicatum**
Amphibromus Nees
Arrhenatherum P. Beauv.
Avena L.
Avena airoides Koel. = **Trisetum spicatum** var. **spicatum**
Avena cernua (Trin.) Kunth = **Trisetum cernuum**
Avena flavescens L. = **Trisetum flavescens**
Avena leptostachys Hook. f. = **Trisetum cernuum**
Avena phleoides d'Urv. = **Trisetum phleoides**
Avena pilosa J. Presl = **Trisetum preslei**
Avena preslei Kunth = **Trisetum preslei**
Bromus L.
Bromus berteroanus Colla
Bromus trinii E. Desv. = **Bromus berteroanus**
Calamagrostis irazuensis Kuntze = **Trisetum irazuense**
Deschampsia P. Beauv.
Deschampsia airiformis (Steud.) Benth. & Hook.f.
Deschampsia andicola (Louis-Marie) Valencia = **Trisetum longiglume** var. **longiglume**
Deschampsia lasiantha Phil. = **Trisetum preslei**
Dielsiochloa Pilg.
Dielsiochloa floribunda (Pilg.) Pilg.
Graphephorum Desv.
Helictotrichon Besser ex Schult. & Schult. f.
Helictotrichon virescens (Nees ex Steud.) Henrard
Koeleria Pers.
Koeleria caudulata (Trin.) Griseb. = **Trisetum caudulatum** var. **caudulatum**
Koeleria cumingii Nees ex Steud. = **Trisetum spicatum** var. **cumingii**
Koeleria fueguina C. E. Calderón ex Nicora
Koeleria lechleri Steud. = **Trisetum caudulatum** var. **caudulatum**
Koeleria spicata Reichb. ex Willk. & Lange = **Trisetum spicatum** var. **spicatum**
Koeleria subspicata (L.) Rchb. = **Trisetum spicatum** var. **spicatum**
Leptophyllochloa C. E. Calderón
Leptophyllochloa micrathera (E. Desv.) C. E. Calderón
Peyritschia E. Fourn.
Peyritschia conferta (Pilg.) Finot
Peyritschia deyeuxioides (Kunth) Finot
Raimundochloa A. M. Molina
Rebentischia Opiz = **Trisetum**
Rebentischia flavescens Opiz = **Trisetum flavescens**
Relchela Steud.
Rostraria Trin.
Rupestrina Prov. = **Trisetum**
Rupestrina pubescens Prov. = **Trisetum spicatum** var. **spicatum**
Sphenopholis Scribn.
Trisetaria airoides (Koeler) Baumg. = **Trisetum spicatum** var. **spicatum**
Trisetaria flavescens (L.) Baumg. = **Trisetum flavescens**
Trisetum Pers.
Trisetum subg. **Deschampsioidea** (Louis-Marie) Finot
Trisetum subg. *Heterolytrum* Louis-Marie = **Trisetum** subg. **Trisetum**
Trisetum subg. *Isolytrum* Louis-Marie = **Trisetum** sect. **Trisetaera**
Trisetum subg. **Trisetum**
Trisetum sect. *Anaulacoa* Louis-Marie = **Trisetum** sect. **Trisetum**
Trisetum sect. *Aulacoa* Louis-Marie = **Dielsiochloa**
Trisetum sect. **Carpatica** Chrtek
Trisetum sect. **Trisetaera** Asch. & Graebn.
Trisetum sect. **Trisetum**
Trisetum subsect. *Carpatica* (Chrtek) Prob. = **Trisetum** sect. **Carpatica**
Trisetum subsect. *Deschampsioidea* Louis-Marie = **Trisetum** subg. **Deschampsioidea**
Trisetum subsect. *Graphephorum* (Desv.) Louis-Marie = **Graphephorum**
Trisetum subsect. *Koeleriformia* Louis-Marie = **Leptophyllochloa**
Trisetum subsect. *Spenopholidea* Louis-Marie = **Sphenopholis**
Trisetum airiforme Steud. = **Deschampsia airiformis**
Trisetum airoides (Koeler) P. Beauv. ex Roem. & Schult. = **Trisetum spicatum** var. **spicatum**
Trisetum albidum Sodiro = **Trisetum spicatum** var. **spicatum**
Trisetum ambiguum Rúgolo & Nicora
Trisetum andicola Louis-Marie = **Trisetum longiglume** var. **longiglume**
Trisetum andinum Benth.
Trisetum araeanthum Phil. = **Leptophyllochloa micrathera**
Trisetum barbatum Steud. = **Bromus berteroanus** Colla
Trisetum barbinode Trin.
Trisetum barbinode Trin. var. **barbinode**
Trisetum barbinode var. **hirtiflorum** (Hack.) Louis-Marie
Trisetum barbinode var. **sclerophyllum** (Hack. ex Stuck.) Finot
Trisetum biflorum Phil. = **Trisetum dianthemum**
Trisetum brachyatherum Phil. = **Leptophyllochloa micrathera**
Trisetum [?] brasiliense Louis-Marie = **Deschampsia brasiliensis** (Louis-Marie) Valencia
Trisetum buchtienii Hack. = **Trisetum preslei**
Trisetum caudulatum Trin.
Trisetum caudulatum Trin. var. **caudulatum**
Trisetum caudulatum var. **correae** Nicora
Trisetum cernuum Trin.
Trisetum chiloense Phil. = **Trisetum caudulatum** var. **caudulatum**
Trisetum chromostachyum E. Desv. = **Trisetum caudulatum** var. **caudulatum**
Trisetum confertum Pilg. = **Peyritschia conferta**
Trisetum cumingii (Nees ex Steud.) Nicora = **Trisetum spicatum** var. **cumingii**

Trisetum cumingii var. *cumingii* = **Trisetum spicatum** var. **cumingii**
Trisetum cumingii var. *santacrucense* Nicora = **Trisetum spicatum** var. **cumingii**
Trisetum depauperatum Phil. = **Leptophyllochloa micrathera**
Trisetum deyeuxioides (Kunth) Kunth
Trisetum dianthemum (Louis-Marie) Finot
Trisetum erectum Phil.—*name of uncertain application*
Trisetum evolutum (E. Fourn.) Hitchc. = **Peyritschia deyeuxioides**
Trisetum flavescens (L.) P. Beauv.
Trisetum flavescens subsp. *pratense* (Pers.) Asch. & Graebn. = **Trisetum flavescens**
Trisetum floribundum Pilg. = **Dielsiochloa floribunda**
Trisetum foliosum Swallen
Trisetum fournieranum Hitchc. = **Trisetum irazuense**
Trisetum fraudulentum Steud. = **Trisetum cernuum**
Trisetum heterogamum Steud. ex Lechler = **Trisetum caudulatum** var. **caudulatum**
Trisetum heteronymum Steud. = **Trisetum caudulatum** var. **caudulatum**
Trisetum hirsutum Phil. = **Trisetum phleoides**
Trisetum hirtiflorum Hack. = **Trisetum barbinode** var. **hirtiflorum**
Trisetum hirtum Trin. = **Bromus berteroanus** Colla
Trisetum irazuense (Kuntze) Hitchc.
Trisetum [?] juergensii Hack.
Trisetum lasiolepis E. Desv. = **Trisetum preslei**
Trisetum laxiflorum Phil. = **Leptophyllochloa micrathera**
Trisetum laxum Phil. = **Leptophyllochloa micrathera**
Trisetum lechleri (Steud.) Nicora = **Trisetum caudulatum** var. **caudulatum**
Trisetum longiglume Hack.
Trisetum longiglume var. **glabratum** Nicora
Trisetum longiglume Hack. var. **longiglume**
Trisetum macbridei Hitchc.
Trisetum malacophyllum Phil. = **Trisetum spicatum** var. **cumingii**
Trisetum malacophyllum Steud. = **Trisetum caudulatum** var. **caudulatum**
Trisetum mattheii Finot
Trisetum micratherum E. Desv. = **Leptophyllochloa micrathera**
Trisetum mollifolium Louis-Marie = **Trisetum spicatum** var. **cumingii**
Trisetum monticola Phil. = **Trisetum caudulatum** var. **caudulatum**
Trisetum nancaguense Finot
Trisetum nemorosum Phil. = **Leptophyllochloa micrathera**
Trisetum ochrostachyum Phil. = **Trisetum caudulatum** var. **caudulatum**
Trisetum oreophilum Louis-Marie
Trisetum oreophilum var. **johnstoni** Louis-Marie
Trisetum oreophilum var. **oreophilum**
Trisetum paradoxum Phil.—*name of uncertain application*
Trisetum phleoides (d'Urv.) Kunth
Trisetum pratense Pers. = **Trisetum flavescens**
Trisetum preslei (Kunth) E. Desv.
Trisetum preslei var. *buchtienii* (Hack.) Louis-Marie = **Trisetum preslei**
Trisetum preslei var. *lasianthum* (Phil.) Louis-Marie = **Trisetum preslei**
Trisetum pyramidatum Louis-Marie ex Finot
Trisetum rosei Scribn. & Merr.
Trisetum scabriflorum Hitchc. = **Trisetum irazuense**
Trisetum sclerophyllum Hack. = **Trisetum barbinode** var. **sclerophyllum**
Trisetum pyramidatum Louis-Marie ex Finot
Trisetum spicatum (L.) K. Richt.
Trisetum spicatum var. **cumingii** (Nees ex Steud.) Finot.
Trisetum spicatum K. Richt. var. **spicatum**
Trisetum spicatum subsp. *andinum* (Benth.) Hultén = **Trisetum andinum**
Trisetum spicatum subsp. *bolivianum* Hultén = **Trisetum spicatum** var. **spicatum**
Trisetum spicatum var. *phleoides* (d'Urv.) Hack. = **Trisetum phleoides**
Trisetum spicatum subsp. *phleoides* (d'Urv.) Hultén = **Trisetum phleoides**
Trisetum spicatum subsp. *phleoides* (d'Urv.) Macloskie = **Trisetum phleoides**
Trisetum spicatum var. *andinum* (Benth.) Louis-Marie = **Trisetum andinum**
Trisetum spicatum var. *dianthemum* Louis-Marie = **Trisetum dianthemum**
Trisetum spicatum var. *hirsutum* Louis-Marie = **Trisetum phleoides**
Trisetum splendidulum Steud. = **Trisetum caudulatum** var. **caudulatum**
Trisetum subspicatum (L.) P. Beauv. = **Trisetum spicatum** var. **spicatum**
Trisetum subspicatum subsp. *phleoides* (d'Urv.) Hack. = **Trisetum phleoides**
Trisetum tomentosum (E. Desv.) Nicora = **Koeleria fueguina**
Trisetum trinii (E. Desv.) Louis-Marie = **Bromus berteroanus** Colla
Trisetum variabile E. Desv. = **Trisetum caudulatum** var. **caudulatum**
Trisetum variabile E. Desv. var. *variabile* = **Trisetum caudulatum** var. **caudulatum**
Trisetum variabile subsp. *virescens* Macloskie = (discussed under T. caudulatum var. caudulatum)
Trisetum variabile var. *chiloense* (Phil.) Louis-Marie = **Trisetum caudulatum** var. **caudulatum**
Trisetum variabile var. *flavescens* E. Desv. = **Trisetum caudulatum** var. **caudulatum**
Trisetum variabile var. *intonsum* Louis-Marie = **Helictotrichon virescens** (Nees ex Steud.) Henrard
Trisetum variabile var. *vidalii* (Phil.) Louis-Marie = **Trisetum caudulatum** var. **caudulatum**
Trisetum variabile var. *virescens* E. Desv. = **Trisetum caudulatum** var. **caudulatum**
Trisetum vidalii Phil. = **Trisetum caudulatum** var. **caudulatum**
Trisetum virescens Nees ex Steud. = **Helictotrichon virescens** (Nees ex Steud.) Henrard
Trisetum weberbaueri Pilg. = **Dielsiochloa floribunda**

MORPHOLOGY OF CYPSELAE IN SUBTRIBE ARCTOTIDINAE (COMPOSITAE–ARCTOTIDEAE) AND ITS TAXONOMIC IMPLICATIONS[1]

R. J. McKenzie,[2] J. Samuel,[2] E. M. Muller,[2] A. K. W. Skinner,[2] and N. P. Barker[2]*

Abstract

Subtribe Arctotidinae comprises an estimated 80–90 species classified in five genera. Taxonomic relationships within the subtribe are poorly understood and the taxonomy of *Arctotis* is notably confused. Cypselar morphology provides a suite of taxonomic characters important at the genus and species levels in Arctotidinae. To help resolve taxonomic relationships in the subtribe, a scanning electron microscopic survey of the cypselae of 40 species from four genera (*Arctotheca*, *Arctotis*, *Cymbonotus*, and *Haplocarpha*) was undertaken. Thirteen informal species groups are distinguished based on cypselar morphology. The results indicate that a reappraisal of the generic concepts of *Arctotis*, *Cymbonotus*, and *Haplocarpha* is warranted. A close affinity is implicated between *Arctotis* sect. *Austro-orientales* and *Cymbonotus*. *Arctotis* species are assigned to nine species groups. Lewin's infrageneric classification of *Arctotis* is partially supported. *Haplocarpha* comprises three disparate species groups. *Arctotheca* forms a morphologically coherent group based on cypselar morphology herein. A diagnostic key to these informal groups based on cypselar morphology is presented.

Key words: *Arctotheca*, *Arctotis*, Asteraceae, *Cymbonotus*, fruit morphology, *Haplocarpha*, scanning electron microscopy, systematics.

Arctotideae comprises about 220 species with a principally southern African distribution. It includes well-known horticultural subjects such as *Arctotis* L. and *Gazania* Gaertn. Two subtribes are currently recognized: Arctotidinae and Gorteriinae (Bremer, 1994). Previous workers have recognized other subtribes such as Gundeliinae (Bentham, 1873a, b, as Gundelieae) and Eremothamninae (Leins, 1970). Molecular studies indicate the Gundeliinae is sister to the Cichorieae Lam. & DC. (Lactuceae Cass.) (Karis et al., 2001; Funk et al., 2004). Recent molecular evidence places *Eremothamnus* O. Hoffm., *Heterolepis* Cass., and *Hoplophyllum* DC. with Arctotideae, but outside Arctotidinae and Gorteriinae (Funk et al., 2004). However, the affinities of these genera indicated by morphological evidence are much less certain (Bremer, 1994; Funk et al., 2004).

A study of plastid and nuclear DNA sequences in Arctotideae provided support for the monophyly of Arctotidinae (Funk et al., 2004). However, some phylogenetically important species of Arctotidinae, such as any representative of *Haplocarpha* subg. *Landtia* (Less.) Beauverd, were not included in their study. Furthermore, identification of morphological synapomorphies for the subtribe remains more difficult. Funk et al. (2004) listed ten morphological traits characterizing Arctotidinae, but noted that seven of those would be considered plesiomorphic, and the absence of latex is probably apomorphic but difficult to utilize at the subtribal level in the subfamily Cichorioideae. This leaves two possible synapomorphies for Arctotidinae: a swelling on the disc-floret style with a ring of sweeping papillae below the apical branches, and 3 to 5 well-developed ridges or wings on the fruits.

As now circumscribed, Arctotidinae comprises approximately 80 to 90 species in five genera (Norlindh, 1977; Bremer, 1994). Most of the species (an estimated 60 to 70 species) belong to *Arctotis*, which is currently under revision in our laboratory. Of the remaining genera, *Arctotheca* J. C. Wendl. contains five species, including the recently described *A. marginata* Beyers (Beyers, 2002). *Haplocarpha* Less. includes nine species, *Dymondia* Compton is monotypic (Compton, 1953; Rourke,

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[2] Department of Botany, Rhodes University, P.O. Box 94, Grahamstown, 6140, South Africa. r.mckenzie@ru.ac.za; n.barker@ru.ac.za.

1974), and the Australian endemic *Cymbonotus* Cass. has two species. A third Australian-endemic species, *Arctotis maidenii*, was treated as *C.* sp. 'A' by Murray (1992). An additional four genera (*Cryptostemma* R. Br., *Landtia* Less., *Microstephium* Less., and *Venidium* Less.) recognized by Harvey (1865) are now included within other genera: *Landtia* was merged with *Haplocarpha*, *Venidium* with *Arctotis* (Beauverd, 1915), and *Cryptostemma* and *Microstephium* with *Arctotheca* (Lewin, 1922a).

A cladistic analysis of morphological characters by Bremer (1994) showed the relationships within Arctotidinae as an unresolved polychotomy. More recent molecular studies (Karis et al., 2001; Funk et al., 2004) have not included sufficient samples to address generic-level relationships, focusing instead on tribal and subtribal relationships. Ongoing morphological and molecular studies in our laboratory indicate generic concepts in Arctotidinae require further resolution. Delimitation of genera is a frequent problem in Compositae (Cronquist, 1985), often reflecting the occurrence of morphologically intermediate taxa or varied combinations of taxonomically important characteristics across a group. Instability in generic classification in Arctotidinae partly reflects differences in the characters emphasized for delimiting genera by different authors. For example, Lessing (1832) emphasized fruit and pappus morphology, ray floret fertility, and filament ornamentation. However, fruit pubescence and pappus characters were found to be unreliable generic criteria in the group and floret fertility received greater emphasis (Beauverd, 1915; Lewin, 1922a).

In addition, considerable confusion exists regarding the taxonomy of *Arctotis*. This partly reflects the brevity of most early species descriptions and a lack of detail on characters now considered to be taxonomically important. Resolution of this confusion will be best achieved by a careful reappraisal of the taxonomic utility of previously utilized characters, a search for additional taxonomically useful characters, and collection of additional specimens of poorly known species. Owing to the previous emphasis placed on fruit morphology (e.g., Lessing, 1832; Harvey, 1865; Beauverd, 1915; Lewin, 1922a), we present here an investigation of the taxonomic utility of fruit morphology in Arctotidinae. Examination of other morphological features and phylogenetic analysis of DNA sequence data are ongoing in our laboratory.

Compositae fruits are termed cypselae. These are indehiscent, one seeded, usually dry, derived from inferior, bicarpellate ovaries, and the testa is adnate to the endocarp (Bremer, 1994). Cypselar morphology was emphasized for classification of Arctotidinae by Lessing (1832), who distinguished eight genera based on cypselar and pappus morphology, ray-floret fertility, and filament ornamentation. Candolle (1837), Harvey (1865), and Bentham (1873a, b) essentially followed Lessing's generic classification. Beauverd (1915) and Lewin (1922a) gave less weight to cypselar pubescence and pappus morphology and greater emphasis to ray-floret fertility to discriminate genera. Both authors used cypselar morphology and filament ornamentation to distinguish infrageneric taxa in *Arctotis* and *Haplocarpha*. Beauverd (1915) recognized four subgenera in *Arctotis* based on cypselar and pappus morphology and distinguished two sections within subgenus *Arctotis* based on growth form. *Landtia* was recognized at subgeneric level within *Haplocarpha* based on pappus characters. Lewin (1922a) recognized 15 sections within *Arctotis* differentiated on the basis of morphology of the cypselae, involucral bracts, and leaves. These sections did not follow previously recognized species groupings. The species formerly segregated as *Venidium* were placed in five sections, and one of those sections (sect. *Acuminatae* K. Lewin) includes a mixture of species that were placed previously in *Venidium* and *Arctotis*.

In Arctotidinae, the cypsela pericarp is very hard and contains a sclerenchymatous layer (Reese, 1989). A diagnostic feature of cypselae in *Arctotis* is the presence of two or three well-developed wings on the abaxial surface; the lateral wings are curved inward creating either one or two furrows or chambers depending on the extent of development of the median wing. Often these furrows or chambers have been termed "cavities" (e.g., Norlindh, 1977; Goldblatt & Manning, 2000), and to avoid confusion this term is retained herein. Cypselar wings are weakly developed in *Cymbonotus* and absent in *Arctotheca* and *Haplocarpha* (Beauverd, 1915; Lewin, 1922a). Instead, cypselae in *Arctotheca* and *Haplocarpha* usually have three to five longitudinal ridges, which are more strongly developed on the abaxial surface. Based on cypsela anatomy, especially pericarp formation and the number of vascular traces, the cypselae of *H. rueppellii* and *H. scaposa* are distinct from those of *Arctotheca*, *Arctotis*, *Cymbonotus*, and *H. lyrata* (Reese 1989). Herman (2001) observed and illustrated three trichome types (multicellular biseriate, septate, and twin hairs) present on the cypselae of *Arctotheca*, *Arctotis*, and *Haplocarpha* species. Twin hairs are a distinctive trichome type widespread in Compositae (Hess, 1938). Some species possess a basal ring of trichomes attached to the carpopodium; such a ring of trichomes is termed a coma by some authors (Hilliard, 1977; Herman, 2001). The pappus, when

present, comprises one or two whorls of free scales in most species; when two whorls are present, the scales are alternately arranged. In some species, the pappus is uniseriate and the scales are at least partially fused at the base, forming a terminal crown (herein termed coronate).

In this paper, cypselae of representative species from each of the genera in Arctotidinae (with the exception of *Dymondia*) are examined by scanning electron microscopy (SEM) with the purpose of identifying "natural" species groups in Arctotidinae based on similarities of external fruit morphology. These groupings will help provide a sound basis for resolution of generic concepts in conjunction with evidence from other sources.

Materials and Methods

Cypselae containing a mature seed were obtained from herbarium specimens and plants in the wild. Cypselae from 4 species of *Arctotheca*, 25 species of *Arctotis* comprising at least one representative from each of Lewin's (1922a) 15 sections, 2 *Cymbonotus* species, and 9 *Haplocarpha* species were examined (Table 1, Appendix 2). Cypselae containing a mature seed were unavailable for study for *Dymondia margaretae* Compton. The South African species recognized generally follow Germishuizen and Meyer (2003). Goldblatt and Manning (2000) treated *A. perfoliata* as a synonym of *A. discolor* (Less.) Beauverd, but the name *A. perfoliata* has nomenclatural priority for the combined taxon.

Cypselae were examined by means of a JEOL JSM 840 Scanning Electron Microscope at the Rhodes University Electron Microscope Unit. All samples were dry and thus were not further treated before being sputter-coated with gold-palladium. In some species the cypselar surface has a dense covering of trichomes or a basal coma, which, in some instances, were removed to allow a clearer vision of the cypselar surface. Supplementary observations of trichome structure were made with a Wild compound microscope.

Cypselar ontogeny was not investigated. It is important to note that cypsela shape, size, and surface features may be influenced by the proportion within a capitulum of cypselae containing a seed and the stage of cypsela development (Breitwieser & Ward, 2003). An additional factor to consider is homology. The ray florets in *Arctotheca* and *Arctotis* sect. *Anomalae* K. Lewin, and the central disc florets in most species of *Arctotis*, are female sterile (Lewin, 1922a). In *A. fastuosa*, the ray and disc florets produce cypselae with minor morphological differences (Beneke et al., 1992). Where available, cypselae containing a mature seed from both ray and disc florets were examined. Because only minor differences in cypselar morphology were noted (principally dimensions and pubescence), separate descriptions of cypselae from both floret types are not presented. Absolute quantitative characters were excluded; two ratios (maximum pappus length: cypsela length and maximum coma length: cypsela length) were included.

Results

SEM micrographs of species examined are shown in Figures 1–7. Selected cypselar characters for all species are summarized in Table 2. Thirteen informal species groups (I–XIII) are recognized herein on the basis of fruit morphology.

Key to the Species Groups in Arctotidinae

1. Prominently raised ridges or wings absent on both abaxial and adaxial surfaces ..... Group I
1′. Abaxial surface with prominently raised ridges or wings 2
2. Abaxial surface with 2 or 3 prominently raised longitudinal ridges 3
2′. Abaxial surface with 2 or 3 distinct wings 5
3. Adaxial surface smooth; pappus well developed, length at least 1.5 × cypsela ..... Group II
3′. Adaxial surface transversely rugose; pappus at most equal in length to cypsela 4
4. Ridges strongly dentate and rugose; uniseriate trichomes present; coma absent ..... Group III
4′. Ridges not dentate or rugose; clothed with septate trichomes often forming woolly indumentum completely concealing cypsela and pappus; coma of either twin hairs or multicellular biseriate trichomes present, neither very distinct from septate trichomes ..... Group IV
5. Wings developed on both abaxial and adaxial surfaces 6
5′. Wings developed on abaxial surface only 7
6. Lateral abaxial wings wide-spreading, median abaxial wing absent, resulting in a single often broad abaxial cavity; adaxial wings very reduced ..... Group V
6′. Lateral abaxial wings strongly incurved, median abaxial wing ± concealed and the two abaxial cavities occluded; adaxial wings well developed, forming two narrow lateral cavities ..... Group VI
7. Cypsela with a single abaxial cavity; median abaxial wing weakly developed ..... Group VII
7′. Cypsela with two abaxial cavities; in some specimens cavities almost occluded by the strongly incurved abaxial wings 8
8. Pappus absent ..... Group VIII
8′. Pappus present 9
9. Cypsela apical plate offset to abaxial side with strongly convex adaxial surface; trichomes simple, uniseriate; pappus scales to 0.25 mm long; coma absent ..... Group IX
9′. Cypsela apical plate not offset to abaxial side; septate trichomes present; maximum pappus

scale length exceeding 0.25 mm long; coma of twin hairs or glandular biseriate trichomes present on carpopodium 10

10. Cypsela wings minutely dentate; sparse septate trichomes to 135 μm long; coma of partial or complete ring of glandular biseriate trichomes on carpopodium; pappus very reduced, with inner whorl of 5 to 7 scales, adaxial scales usually absent, sometimes with rudimentary scales of outer whorl on abaxial side ..... Group X

10′. Cypsela with entire or dentate wings; glabrous or with septate trichomes exceeding 135 μm long; coma of twin hairs present; pappus in 2 whorls, inner whorl much longer than outer whorl 11

11. Cypsela wings fused to median abaxial rib in proximal part; cypsela base constricted; abaxial cavities ovate ..... Group XI

11′. Cypsela wings not fused to median abaxial rib in proximal part; cypsela base not constricted; abaxial cavites obconical, obovate, or linear ... 12

12. Lengths of pappus scales and coma less than half the cypsela ..... Group XII

12′. Lengths of pappus scales and coma subequal or longer than cypsela ..... Group XIII

SPECIES GROUP I

Haplocarpha hastata (Fig. 1A), *H. nervosa* (Fig. 1B), *H. rueppellii* (Fig. 1C)

The species group comprises three species assignable to *Haplocarpha* subg. *Landtia*. The cypselae have a smooth surface, a very reduced pappus, and lack prominent abaxial ridges or wings. The cypselae are obovoid in *H. nervosa* and obovoid-elliptic in *H. hastata* and *H. rueppellii*; the cypsela base is constricted in *H. rueppellii*. The cypselae are tangentially flattened in *H. hastata*, but in *H. nervosa* and *H. rueppellii* the cypselae are somewhat 3- or 4-angled; in each species the adaxial surface is more strongly convex than the abaxial surface. The cypselar surface is smooth in *H. hastata* and *H. rueppellii*; in some specimens of *H. nervosa* the surface is transversely rugose. The cypselae are glabrous in *H. hastata* and *H. rueppellii*; either biseriate glandular trichomes or uniseriate trichomes to 125 μm long are present on cypselae in *H. nervosa*. A coma of twin hairs to 1 mm long is present in *H. nervosa* and is lacking in *H. hastata* and *H. rueppellii*. The pappus is coronate with indistinct lobes in *H. hastata*. *Haplocarpha nervosa* and *H. rueppellii* have a pappus of scales in 2 whorls, the scales of each whorl alternate with those of the other whorl. In *H. nervosa*, the inner whorl (0.3–0.5 mm long) is slightly longer than the outer whorl (0.2–0.3 mm long); in *H. rueppellii* the scales are of uniform lengths.

SPECIES GROUP II

Haplocarpha lanata (Fig. 1E, F), *H. lyrata* (Fig. 1D), *H. oocephala* (Fig. 1G), *H. parvifolia*, *H. scaposa* (Fig. 1H)

The species group comprises four species placed in *Haplocarpha* subg. *Haplocarpha* by Beauverd (1915) and *H. oocephala*, which was recently transferred to *Haplocarpha* from *Arctotis* (Beyers 2000). The cypselae are broadly obconical in *H. scaposa* and obconical in the other species, tangentially flattened in *H. lanata*, *H. lyrata*, and *H. scaposa*, with well-developed abaxial ridges, a coma of twin hairs, and a pappus of scales in 1 or 2 whorls, which is always longer than the cypsela. The ridges are least developed in *H. scaposa*. In *H. lyrata* the lateral abaxial ridges are shortly incurved toward the median ridge (most evident in transverse section). The ridges are very broad and separated by narrow furrows in *H. oocephala* and *H. parvifolia*. The ridges are transversely rugose in *H. oocephala* and smooth in the other species. The adaxial surface is smooth in all species. The cypsela surface is glabrous in *H. scaposa*. Dense twin hairs are present on both abaxial and adaxial surfaces in *H. lanata* and *H. lyrata*. Glandular biseriate trichomes are present on the abaxial ridges in *H. oocephala* and *H. parvifolia*. All species possess a coma of twin hairs; the coma is subequal to the cypsela in *H. lanata* and *H. lyrata*, up to double the cypsela length in *H. oocephala* and *H. parvifolia*, and more than triple the cypsela length in *H. scaposa*. There are 2 pappus whorls present in *H. oocephala*, *H. parvifolia*, and *H. scaposa*, of which the inner whorl is much longer than the outer whorl; only the inner pappus whorl (as indicated by the alignment of the scales with the cypsela ridges) is present in *H. lanata* and *H. lyrata*. The pappus scale apices are acuminate in *H. lyrata* and *H. scaposa*, acute in *H. lanata*, and obtuse to rounded in *H. oocephala* and *H. parvifolia*. The scale apex is serrate in *H. lanata* and *H. lyrata*. The scales are more than 4 times the cypsela length in *H. scaposa* and 1.5 to 2 times the cypsela length in the other species.

SPECIES GROUP III

Haplocarpha schimperi (Fig. 2A–C)

On the basis of external cypselar morphology, *Haplocarpha schimperi* is anomalous within *H.* subg. *Landtia*. The cypselae are obovoid, tangentially flattened with 3 well-developed, dentate abaxial ridges, transversely rugose on both abaxial and adaxial surfaces, with uniseriate trichomes to 75 μm long and a short pappus. A coma is absent.

Table 1. Species of Arctotidinae investigated. Lewin's (1922a) infrageneric classification of *Arctotis* and Beauverd's (1915) infrageneric classification of *Haplocarpha* are followed. The informal species group to which each species is assigned in this paper is given in parentheses.

Genus	Subgenus/section	Species
Arctotheca J. C. Wendl. (4 of 5 spp. sampled)		*A. calendula* (L.) Levyns (IV)
		A. calendula (L.) Levyns × *A. populifolia* (P. J. Bergius) Norl. (IV)
		A. forbesiana (DC.) K. Lewin (IV)
		A. populifolia (P. J. Bergius) Norl. (IV)
		A. prostrata (Salisb.) Britten (IV)
Arctotis L. (25 of ca. 60–70 spp. sampled)	sect. *Acaules* K. Lewin	*A. acaulis* L. (XI)
	sect. *Acuminatae* K. Lewin	*A. semipapposa* (DC.) Beauverd (X)
	sect. *Adpressae* K. Lewin	*A. verbascifolia* Harv. (XI)
	sect. *Aequales* K. Lewin	*A. campanulata* DC. (XIII)
	sect. *Angustifoliae* K. Lewin	*A. angustifolia* L. (XIII)
	sect. *Anomalae* K. Lewin	*A. dregei* Turcz. (V)
	sect. *Argentae* K. Lewin	*A. argentea* Thunb. (XIII)
	sect. *Asperae* K. Lewin	*A. aspera* L. var. *aspera* (XIII)
	sect. *Austro-orientales* K. Lewin	*A. arctotoides* (L. f.) O. Hoffm. (VII)
		A. hispidula (Less.) Beauverd (VII)
		A. microcephala (DC.) Beauverd (VII)
		A. perfoliata (L. f.) O. Hoffm. (VIII)
		A. suffruticosa K. Lewin (VII)
	sect. *Caudatae* K. Lewin	*A. fastuosa* Jacq. (VII)
	sect. *Cuneatae* K. Lewin	*A. cuneata* DC. (XIII)
		A. rotundifolia K. Lewin (XIII)
	sect. *Hirsutae* K. Lewin	*A. hirsuta* (Harv.) Beauverd (IX)
	sect. *Leptorhizae* K. Lewin	*A. breviscapa* Thunb. (VI)
	sect. *Revolutae* K. Lewin	*A. cuprea* Jacq. (XIII)
		A. graminea K. Lewin (XII)
	sect. *Stoechadinae* K. Lewin	*A. venusta* Norl. (XIII)
	Not assigned to a section:	*A. gumbletonii* Hook. f. (XIII)
		A. maidenii Beauverd (VIII)
		A. scapiformis Thell. (VII)
		A. scullyi Dümmer (XIII)
Cymbonotus Cass. (2 of 2 spp. sampled)		*C. lawsonianus* Gaudich. (VII)
		C. preissianus Steetz (VII)
Haplocarpha Less. (9 of 9 spp. sampled)	subg. *Haplocarpha*	*H. lanata* Less. (II)
		H. lyrata Harv. (II)
		H. parvifolia (Schltr.) Beauverd (II)
		H. scaposa Harv. (II)
	subg. *Landtia* (Less.) Beauverd	*H. nervosa* (Thunb.) Beauverd (I)
		H. rueppellii (Sch. Bip.) Beauverd (I)
		H. schimperi (Sch. Bip.) Beauverd (III)
	Not assigned to a subgenus:	*H. hastata* K. Lewin (I)
		H. oocephala (DC.) Beyers (II)

The uniseriate pappus may comprise 8 free scales (*M. Thulin 1609* [ETH]) or be coronate with all scales fused in the lower 2/3 (*N. P. Barker 1899* [ETH, GRA]). The pappus is up to 1/4 the cypsela length.

SPECIES GROUP IV

Arctotheca calendula (Fig. 2D–F), *A. forbesiana*, *A. prostrata* (Fig. 2G, H), *A. populifolia* (Fig. 3A–C).

The species group consists of the four *Arctotheca* species examined. The cypselae are obovoid-elliptic, tangentially flattened, with 2 or 3 abaxial ridges and 2 adaxial ridges, the cypsela surface is transversely rugose with septate trichomes, when present the coma is composed of twin hairs or multicellular biseriate trichomes, but neither is very distinct from the septate trichomes, and the pappus, when present, forms a single whorl and is usually shorter than the cypsela. The cypselae are more strongly

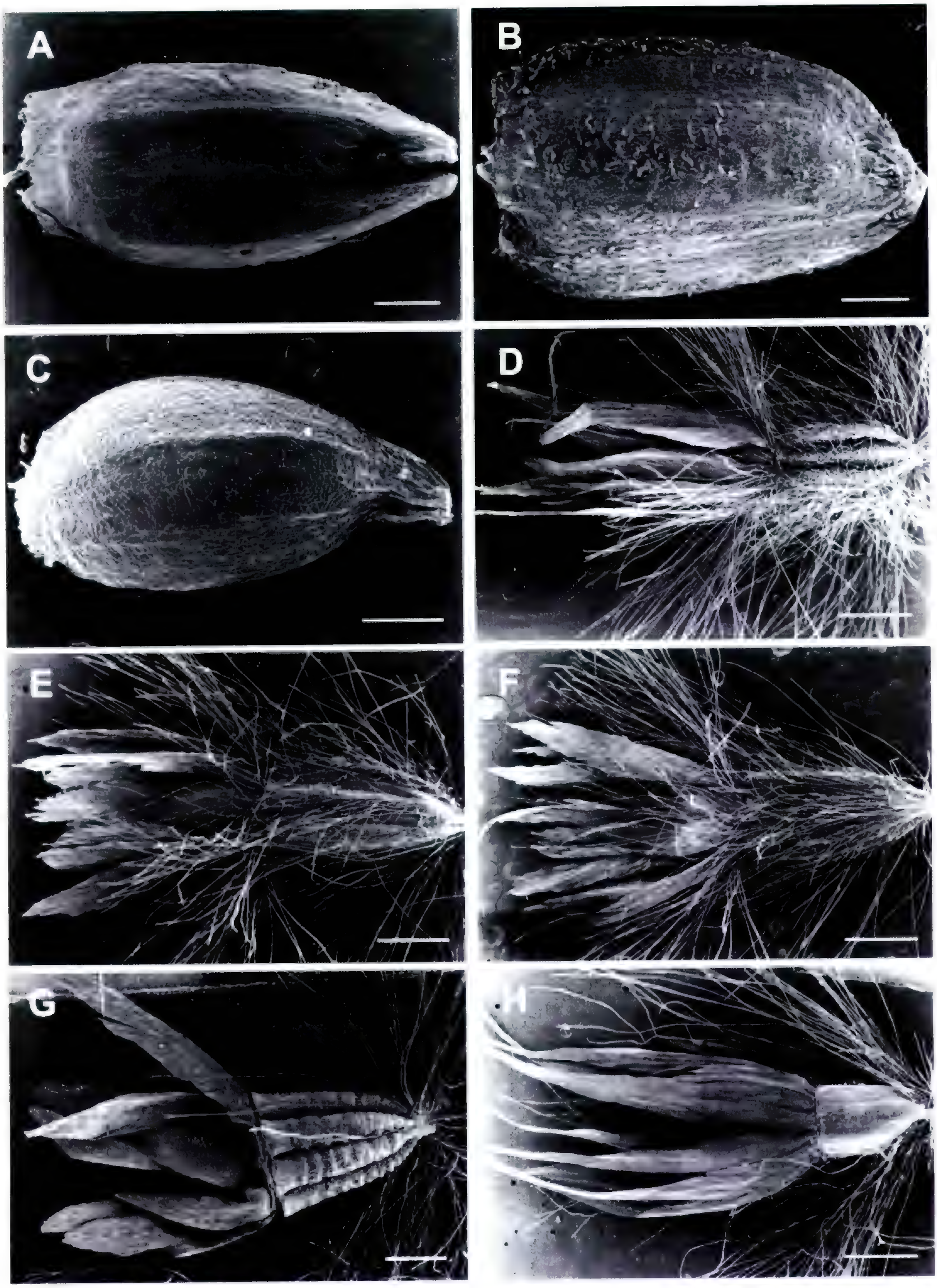

Figure 1. Cypselae of Arctotidinae. —A. *Haplocarpha hastata, J. W. Ash 1700*, abaxial surface. Scale bar = 500 µm. —B. *H. nervosa, R. A. Dyer 786*, abaxial surface. Scale bar = 500 µm. —C. *H. rueppellii, M. Thulin, A. Hunde & M. Tadesse 3715*, abaxial surface. Scale bar = 500 µm. —D. *H. lyrata, R. J. McKenzie 1116*, abaxial surface (twin hairs partially removed). Scale bar = 1 mm. —E. *H. lanata, E. J. Kruger 441*, abaxial surface (twin hairs partially removed). Scale bar = 1 mm. —F. *H. lanata, E. J. Kruger 441*, adaxial surface. Scale bar = 1 mm. —G. *H. oocephala, E. E. Esterhuysen 34661*, abaxial surface. Scale bar = 1 mm. —H. *Haplocarpha scaposa, R. J. McKenzie 909/4*, abaxial surface. Scale bar = 1 mm.

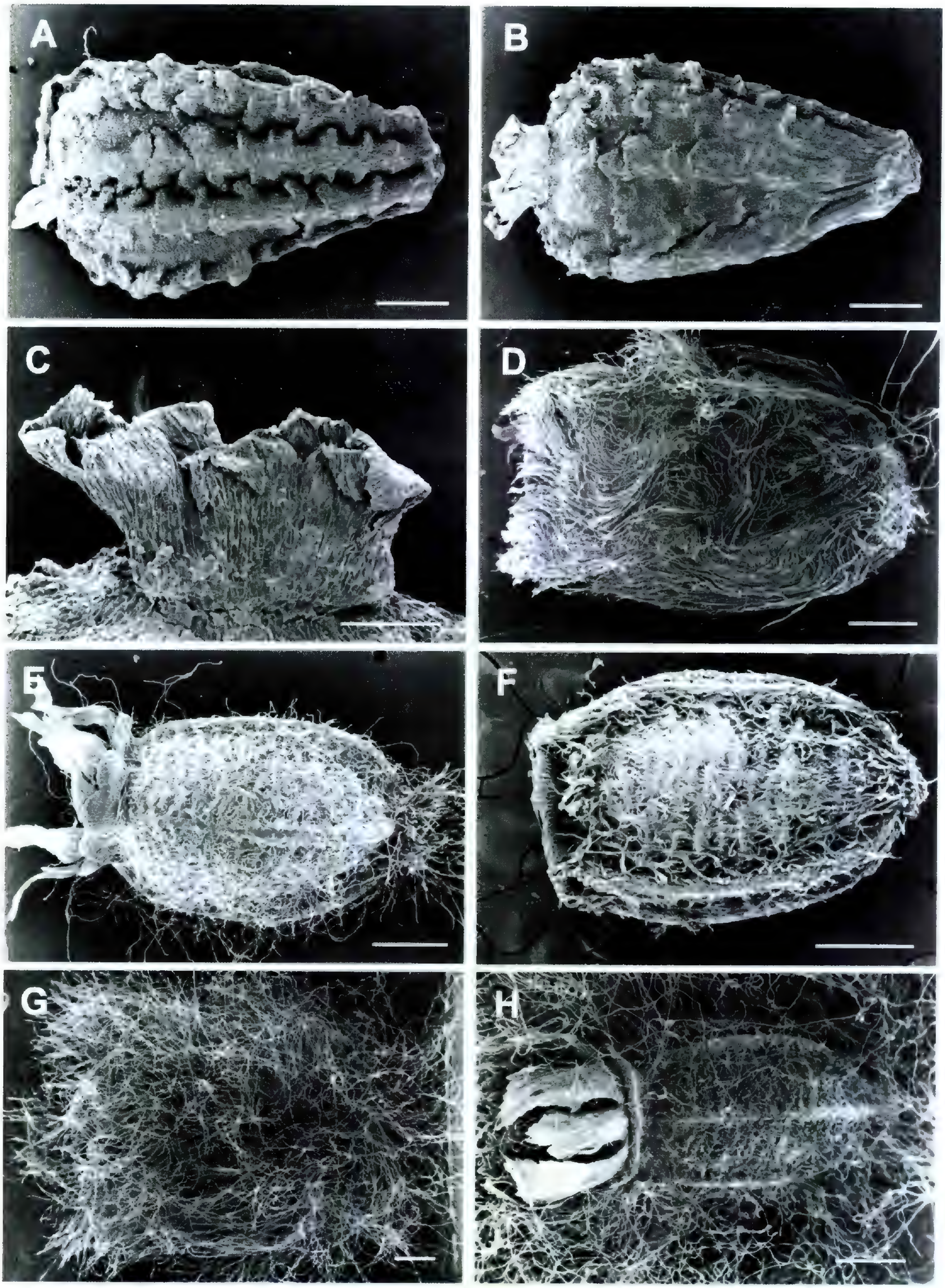

Figure 2. Cypselae of Arctotidinae. —A. *Haplocarpha schimperi, N. P. Barker 1899* (GRA), abaxial surface. Scale bar = 500 μm. —B. *H. schimperi, N. P. Barker 1899* (GRA), adaxial surface. Scale bar = 500 μm. —C. *H. schimperi. N. P. Barker 1899* (GRA), pappus. Scale bar = 200 μm. —D. *Arctotheca calendula, R. J. McKenzie 808/3*, abaxial surface. Scale bar = 500 μm. —E. *A. calendula, R. J. McKenzie 808/3*, abaxial surface (trichomes removed). Scale bar = 500 μm. —F. *A. calendula, P. A. Bean 2992*, abaxial surface. Scale bar = 500 μm. —G. *A. prostrata, R. J. McKenzie 1129*, abaxial surface. Scale bar = 500 μm. —H. *A. prostrata, R. J. McKenzie 1129*, abaxial surface (trichomes removed). Scale bar = 500 μm.

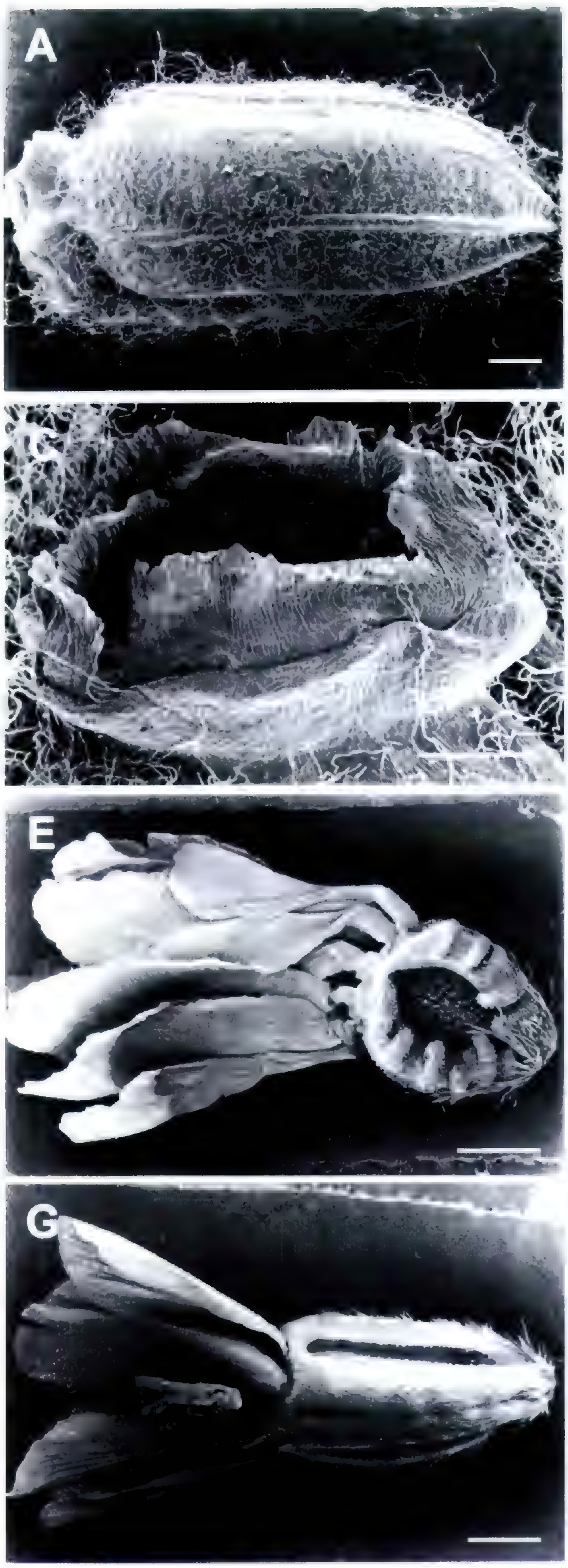

Figure 3. Cypselae of Arctotidinae. —A. *Arctotheca populifolia, R. J. McKenzie 771*, abaxial surface (trichomes removed). Scale bar = 500 μm. —B. *A. populifolia, R. J. McKenzie 771*, adaxial surface (trichomes removed). Scale bar = 500 μm. —C. *A. populifolia, R. J. McKenzie 771*, pappus. Scale bar = 500 μm. —D. *Arctotis dregei, R. J. McKenzie 831/1*, abaxial surface. Scale bar = 1 mm. —E. *A. dregei, R. J. McKenzie 815/2*, abaxial surface. Scale bar = 1 mm. —F. *A. dregei, R. J. McKenzie 815/2*, adaxial surface. Scale bar = 1 mm. —G. *Arctotis breviscapa, C. Boucher & P. Shepherd 160*, abaxial surface. Scale bar = 1 mm. —H. *A. breviscapa, J. A. Marsh 1214*, adaxial surface. Scale bar = 500 μm.

convex on the abaxial surface than the adaxial surface, particularly in *A. populifolia*. The position of the prominent ridges is variable; the lateral abaxial ridges may be inconspicuous in *A. calendula*; the median abaxial ridge may be inconspicuous in *A. calendula* (Fig. 2F), *A. populifolia*, and *A. prostrata*. Septate trichomes often form a dense woolly indumentum completely concealing the cypsela and pappus if present, but in some *A. calendula* and *A. prostrata* specimens the indumentum is sparse. A coma of multicellular biseriate trichomes is present in *A. calendula*. In *A. forbesiana* and *A. prostrata* the coma comprises long, thread-like twin hairs. The coma is about 1/5 of the cypsela length in *A. populifolia* and is of similar length to the cypsela in the other species. A pappus may be absent in *A. calendula* (Fig. 2F) and *A. prostrata*. In *A. calendula* the pappus, when present, is of two forms: either 2 lateral obovate to oblanceolate scales with often a third much reduced adaxial scale; or a whorl of 7 to 9 scales of similar length (e.g., *C. Cottrell 7* [GRA]). The pappus comprises a whorl of 8 or 9 scales in *A. forbesiana* and a whorl of 7 to 9 scales when present in *A. prostrata*. The pappus is always coronate in *A. populifolia* with 7 to 11 lobes, but the degree of scale fusion is variable; some scales may be completely free but are usually fused in at least the basal half. The pappus is very reduced in *A. populifolia* (0.25–0.5 mm long, up to 0.15 × cypsela length). In the other species the pappus consists of scales to 1.3 mm long; in *A. prostrata* the scales may be of similar length to the cypsela, but are usually more reduced. In all species the rim of the apical plate forms a shallow, lobed cup around the base of the pappus (Fig. 2F, 3C).

SPECIES GROUP V

Arctotis dregei (Fig. 3D–F)

This species is assigned to *Arctotis* sect. *Anomalae*. The cypselae are obovoid-elliptic, tangentially flattened, with 2 wide-spreading abaxial wings creating a single elliptic-sinuate to linear-sinuate abaxial cavity, 2 short adaxial wings (most evident in transverse section), a coma of twin hairs, and a pappus of scales in 2 whorls. In some specimens a weakly raised median abaxial ridge is present in the cavity, but is never developed into a wing. In some specimens the abaxial cavity is narrow (Fig. 3D), but usually the cavity is very broad (Fig. 3E). The abaxial wings are transversely rugose and bear rounded-truncate teeth; the adaxial wings are not rugose or dentate. Unicellular trichomes are dense on the abaxial wings and sparse to dense within the cavity. On the adaxial surface uniseriate trichomes are usually moderate-dense on the upper part and the adaxial wings, and glabrous in the center and lower part; in some specimens the adaxial surface is entirely glabrous. The coma comprises a ring of twin hairs, 1/5 to equal the cypsela length, notably longer on the adaxial surface. The inner pappus whorl of 8 or 9 scales is longer than the outer whorl and varies in length from 0.5 to 1.5 times the cypsela length. The outer whorl consists of 6 to 9 scales; when the whorl is incomplete, scales are absent on the abaxial side. The scale apex is obtuse to rounded in the inner whorl and acute to obtuse in the outer whorl.

SPECIES GROUP VI

Arctotis breviscapa (Fig. 3G, H)

This species is assigned to *Arctotis* sect. *Leptorhizae*. The cypselae are unique in having 2 well-developed adaxial wings, in addition to 3 abaxial wings. The cypselae are oblanceolate-compressed, with a short coma of twin hairs and a uniseriate pappus of 8 scales. The lateral abaxial wings are strongly incurved, usually occluding the abaxial cavities and concealing the median abaxial wing. Both the abaxial and adaxial wings are entire. The adaxial cavities are linear. Dense, short septate trichomes to 100 μm long are present on the abaxial and lateral surfaces. Dense unicellular trichomes cover the adaxial surface between the adaxial wings. Papillose trichomes are present on both surfaces in some specimens (e.g., *C. Boucher & P. Shepherd 4602* [NBG, PRE]). The coma is up to 1/4 the cypsela length. The pappus is at most equal in length to the cypsela. The pappus scale apex is rounded.

SPECIES GROUP VII

Arctotis arctotoides (Fig. 4A, B), *A. fastuosa* (Fig. 4C, D), *A. hispidula*, *A. microcephala* (Fig. 4E, F), *A. scapiformis* (Fig. 4G, H), *A. suffruticosa*, *Cymbonotus lawsonianus* (Fig. 5A, B), *C. preissianus* (Fig. 5C, D)

This group contains five species assignable to *Arctotis* sect. *Austro-orientales*, *A. fastuosa*, and the two species of *Cymbonotus*. The cypselae in this group have 2 or 3 abaxial wings, a single linear or sinuate-linear abaxial cavity, simple uniseriate trichomes or biseriate glandular trichomes, a coma of twin hairs is absent, and a pappus is present in two forms of *A. fastuosa*. Two adaxial ridges are usually present; one or additional adaxial ridges may occur in *A. microcephala* and *A. scapiformis*. The cypselae

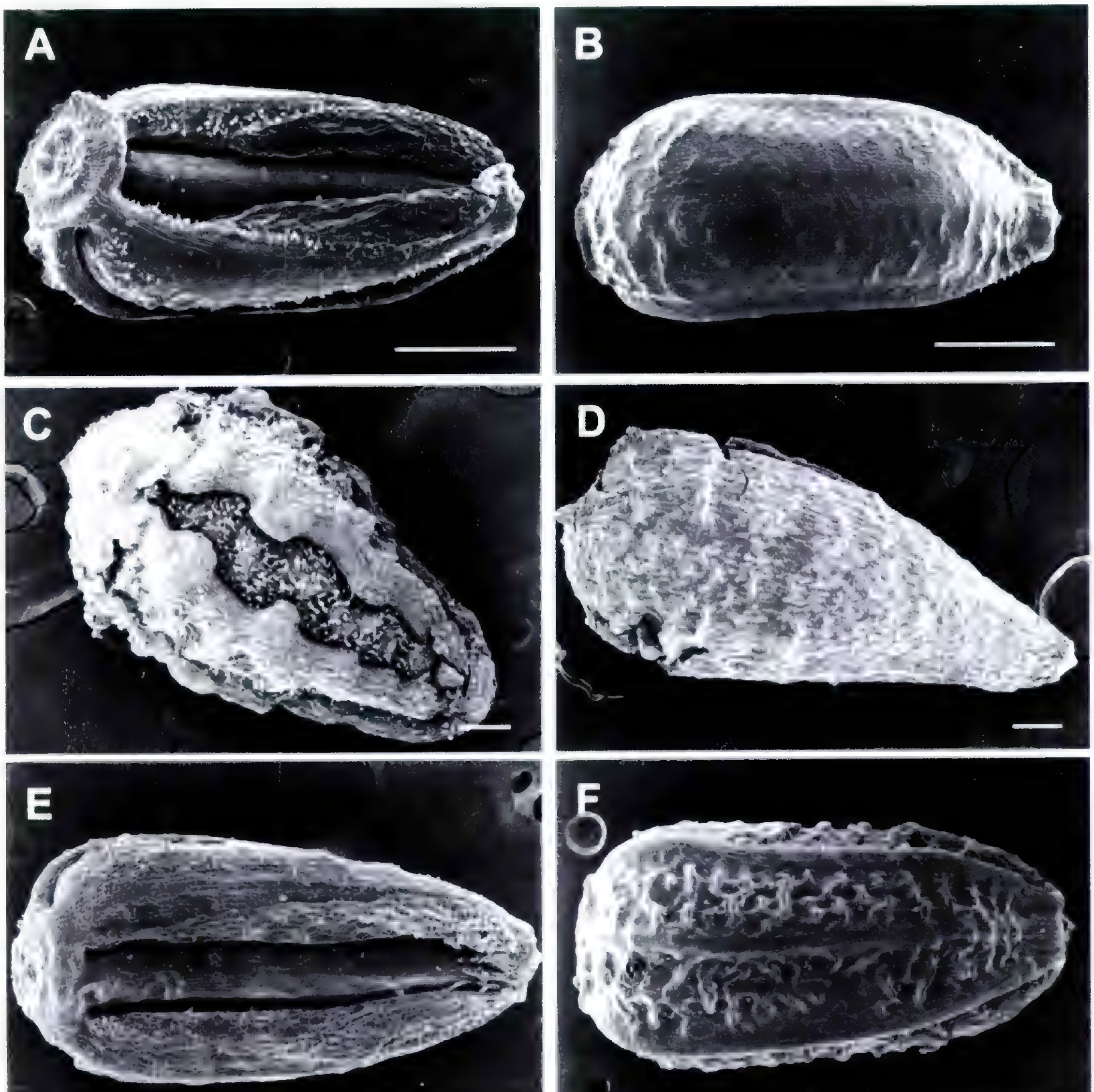

Figure 4. Cypselae of Arctotidinae. —A. *Arctotis arctotoides*, *R. J. McKenzie 724/1*, abaxial surface. Scale bar = 500 μm. —B. *A. arctotoides*, *R. J. McKenzie 724/1*, adaxial surface. Scale bar = 500 μm. —C. *A. fastuosa*, *J. Hutchinson 889*, abaxial surface. Scale bar = 200 μm. —D. *A. fastuosa*, *J. Hutchinson 889*, adaxial surface. Scale bar = 200 μm. —E. *A. microcephala*, *W. J. Hanekom 1963*, abaxial surface. Scale bar = 500 μm. —F. *A. microcephala*, *W. J. Hanekom 1963*, adaxial surface. Scale bar = 500 μm. —G. *A. scapiformis*, *A. White 41*, abaxial surface. Scale bar = 500 μm. —H. *A. scapiformis*, *A. White 41*, adaxial surface. Scale bar = 500 μm.

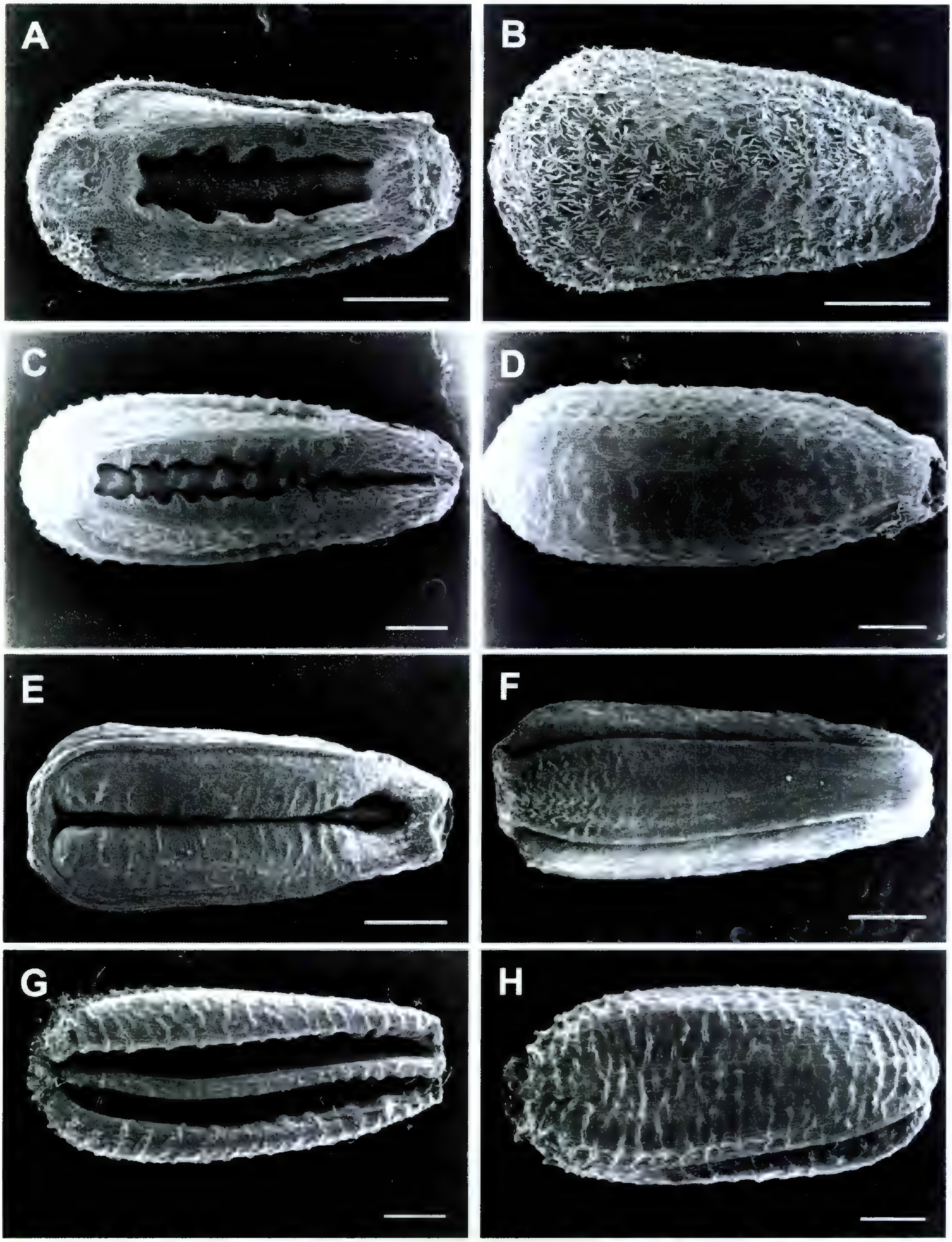

Figure 5. Cypselae of Arctotidinae. —A. *Cymbonotus lawsonianus, J. M. Dalby 86/128*, abaxial surface. Scale bar = 500 μm. —B. *C. lawsonianus, J. M. Dalby 86/128*, adaxial surface. Scale bar = 500 μm. —C. *C. preissianus, H. Salasoo 2113*, abaxial surface. Scale bar = 500 μm. —D. *C. preissianus, H. Salasoo 2113*, adaxial surface. Scale bar = 500 μm. —E. *Arctotis maidenii, T. J. Whaite 3787*, abaxial surface. Scale bar = 1 mm. —F. *A. maidenii, T. J. Whaite 3787*, adaxial surface. Scale bar = 1 mm. —G. *A. perfoliata, W. E. Dix 156*, abaxial surface. Scale bar = 500 μm. —H. *A. perfoliata, W. E. Dix 156*, adaxial surface. Scale bar = 500 μm.

Table 2. Selected cypselar morphological characters for Arctotidinae examined. See Appendix 1 for key to the characters. The informal species group to which each species is allocated in this paper is given in parentheses. NA = character is not applicable.

Species	1	2	3	4	5	6	7	8	9	10	11	12
Arctotheca calendula (IV)	3	1	0	3	1	1	1	0	0	0	NA	NA
A. forbesiana (IV)	2	1	0	3	1	1	2	0	0	0	NA	NA
A. populifolia (IV)	3	1	0	3	0	1	1	0	0	0	NA	NA
A. prostrata (IV)	3	1	0	3	0	1	1	0	0	0	NA	NA
Arctotis acaulis (XI)	5	0	1	0	1	0/1	2/3	1	2	0	7	1/2
A. angustifolia (XIII)	1	0	0	0	1	0	2/3	1	2	0	6	1
A. arctotoides (VII)	2	0	0	3	2	0/1	1	1	1	0	2	1/2
A. argentea (XIII)	1	0	0	0	1	0	2	1	2	0	4	1/2
A. aspera var. *aspera* (XIII)	1	0	0	0	1	0	2	1	2	0	2	2
A. breviscapa (VI)	4	0	0	0	1	0	1	2	0	2	NA	1
A. campanulata (XIII)	1	0	0	0	1	0	2	1	2	0	3	1
A. cuneata (XIII)	1	1	0	0	1	0/1	2	1	2	0	3/4	1/2
A. cuprea (XIII)	1	0	0	0	1	0	2	1	2	0	3	2
A. dregei (V)	3	1	0	1	0/1	0	1	2	1	2	1/2	2
A. fastuosa (VII)	2	1	0	3	0	0	1	1	1	0	2	2
A. graminea (XII)	4	0	0	0	1	0	1	1	2	0	3	1
A. gumbletonii (XIII)	1	0	0	0	1	0	2	1	2	0	3	2
A. hirsuta (IX)	2	0	1	1	1	1	3	1	2	0	6	1/2
A. hispidula (VII)	2	0	0	3	2	0/1	2	1	2	0	3/4	1/2
A. maidenii (VIII)	2	1	0	1/2	1	0	1	1	1	0	5	1/2
A. microcephala (VII)	2	0	0	3	2	1	1	1	1	0	2	1
A. perfoliata (VIII)	4	0	0	3	1	0/1	1/2	1	1/2	0	2/5	1
A. rotundifolia (XIII)	1	0	0	0	1	1	2	1	2	0	3	1/2
A. scapiformis (VII)	2	0	0	2	2	1	1	1	1	0	2	1
A. scullyi (XIII)	1	0	0	0	1	0	1/2	1	2	0	2/4	1/2
A. semipapposa (X)	5	0	0	0	1	0	2	1	2	0	2	2
A. suffruticosa (VII)	2	0	0	3	2	1	1	1	1	0	2	1
A. venusta (XIII)	2	0	0	0/1	1	0	2	1	2	0	2	1/2
A. verbascifolia (IX)	4	0	1	0	1	0	2	1	2	0	3	1
C. lawsonianus (VII)	2	0	0	3	2	0	1	1	1	0	2	2
C. preissianus (VII)	2	0/1	0	3	2	1	1	1	1	0	2	2
H. hastata (I)	2	1	1	0	1	0	2	0	0	0	NA	NA
H. lanata (II)	5	0	0	0	1	0	2	0	0	0	NA	NA
H. lyrata (II)	5	0	0	0	1	0	2	1	0	0	2	1
H. nervosa (I)	2	0	0	0	1	0	2	0	0	0	NA	NA
H. oocephala (II)	1	0	0	1	2	1	2	0	0	0	NA	NA
H. parvifolia (II)	1	0	0	0	2	1	2	0	0	0	NA	NA
H. rueppellii (I)	2	0	1	0	1	0	2	0	0	0	NA	NA
H. scaposa (II)	1	0	0	0	1	0	2	0	0	0	NA	NA
H. schimperi (III)	2	0	0	3	2	1	2	0	0	0	NA	NA

are obconical in *A. fastuosa* and obovoid or obovoid-cylindrical in the other species. The cypsela is radially curved with a concave abaxial surface and convex adaxial surface in some specimens of *A. fastuosa*, *A. hispidula*, and *C. lawsonianus*. The surface is transversely rugose only on the abaxial surface in *A. scapiformis* and some specimens of *A. fastuosa*, and on both abaxial and adaxial surfaces in the other species. The abaxial wings are only weakly to moderately developed and strongly incurved, and the median wing or ridge is always shorter than the lateral ones. The abaxial wings are least developed in a form of *A. fastuosa* (Fig. 4C). The wings may be entire or dentate and the shape of the teeth ranges from acute to truncate (Table 2). Teeth were not observed in *A. microcephala* and *A. scapiformis*. Only simple unicellular or uniseriate trichomes (to 30 μm long) are present on the cypsela surface; papillose trichomes are common in *C. preissianus*. A coma of twin hairs is absent in all specimens examined. Instead, one or a few biseriate glandular trichomes are present on the carpo-

Table 2. Extended.

13	14	15	16	17	18	19	20	21	22
NA	NA	1	2/3	3	1	1	1/2	0	0/1
NA	NA	1	3	3	1	1–1.2	1	0	1
NA	NA	1	2/3	2/3	1	0.2	1	0	1
NA	NA	1	2/3	2/3	1	1	1	0	0/1
1	1	1	0/2/3	0/2/3	1	1–1.4	1	1	2
NA	1	1/5	1/2	3	1	1.25–1.4	1	1	2
3/4	2	2	0/1/2	0/1/2	2	NA	3	0	0
1	2	1	3	3	1	1–1.5	1	1	2
2/3	2	1	3	3	0	1.2–1.5	1	0	2
NA	3	2/5	3	3	1	0.1–0.25	1	0	1
NA	1	1	1/2	3	1	0.8–1.1	1	1	2
1	2	1	0/2	3	1	0.75–1.3	1	1	2
1	1	1	3	3	1	1.6–1.9	1	1	2
2/3/4	1/2	2	3	0/1	1	0.75–1	1	1	2
2/3	1	2	1/2	2/3	0	NA	NA	1	0
NA	1	1	2	1	1	0.15–0.3	1	1	2
1/2	1	NA	NA	NA	1	1–1.5	1	0	2
2	1	6	1	3	0	NA	NA	1	1
1	2	2	1/2	1/2	2	NA	3	0	0
1/2	3	2	0	1/2	2	NA	3	0	0
NA	2	2	1	1	2	NA	3	0	0
NA	2	NA	NA	NA	0	NA	NA	0	0
1/2/3	2	1	0/3	3	1	0.3–0.5	1	1	2
NA	2	NA	NA	NA	2	NA	3	0	0
2/3	2/3	1	1/3	3	1	1.5–2	1	1	2
1/2/3	1	1	1	1	1/2	<0.05	3	0	1/2
NA	2	2	2	2	2	NA	3	0	0
1	1	1	1/2	3	1	1.25–1.5	1	1	2
NA	1	1	2/3	3	1	1.25–1.3	1	1	2
2/3	2	2	1	3	0	NA	NA	0	0
1/2/3	2	2	3	3	0/3	NA	3	0	0
NA	NA	NA	0	0	0	NA	NA	0	1
NA	NA	3	2	2	1	0.75–1	1	0	1
NA	1	3	3	3	1	0.75–1	1	0	1
NA	NA	2/4	2/3	2/3	1	0.1–0.15	1	0	2
NA	NA	4	1/2	0	1	1.5–1.75	1	1	2
NA	NA	4	2	0	1	1.75–2	1	1	2
NA	NA	NA	0	0	0	NA	NA	0	2
NA	NA	NA	0	0	1	3.5	1	0	2
NA	NA	2	1	1	0	NA	NA	0	1

podium on the abaxial surface (usually between the abaxial wings) in *A.* sect. *Austro-orientales* species or on the adaxial surface in some *C. preissianus* specimens. No trichomes were observed on the carpopodium in *A. fastuosa* and *C. lawsonianus*. In *A. fastuosa* the pappus, when present, consists of either a single whorl of 2 to 7 scales to 0.15 mm long, or 2 whorls of 1 to 4 and 7 to 9 scales respectively, with the longest scales (to 0.3 mm long) on the adaxial surface.

SPECIES GROUP VIII

Arctotis maidenii (Fig. 5E, F), *A. perfoliata* (Fig. 5G, H)

Based on cypselar morphology *Arctotis perfoliata* is anomalous within *A.* sect. *Austro-orientales*; *A. maidenii* has not been assigned to a section. Both species have large obovoid, tangentially flattened cypselae with 3 abaxial wings and 2 adaxial ridges, and lack a coma of twin hairs and a pappus. The

Table 2. Extended.

23	24	25	26	27	28	29
0	2–9	NA	0.2–0.7	0	1	1/2
0	8–9	NA	0.25–0.3	0	1	2
0	7–11	NA	0.05–0.15	1	NA	3
0	7–9	NA	0.4–1	0	1	1/2
8	8	2	1–1.9	0	2	3
c.5	8	2	0.35–0.85	0	1	2/3
NA	NA	NA	NA	NA	NA	NA
8	8	2	1–1.5	0	2	3
8	8	2	1.5–1.7	0	2	2/3
0	8	NA	0.75–1	0	2	3
8	8	2	1.25–1.4	0	2	2/3
8	8	2	1.25–1.9	0	2	2/3
8	8	2	1.7–1.9	0	2	2/3
6–9	8–9	2	0.5–1.6	0	1	2/3
NA	NA	NA	NA	NA	NA	NA
8	8	2	0.3	0	2	3
8	8	2	1.5–2	0	2	3
0	8	NA	0.04–0.06	0	1	3
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
8	8	2	1.25–1.5	0	2	3
NA	NA	NA	NA	NA	NA	NA
8	8	2	1.25–1.7	0	2	2/3
0–c.10	5–8	2	0.03–0.25	0	1	2/3
NA	NA	NA	NA	NA	NA	NA
8	8	2	1–1.5	0	2	2
8	8	2	1.25–1.8	0	2	2/3
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	NA	NA	NA	NA
NA	NA	NA	0.1	1	NA	NA
0	9	NA	1–1.4	0	1	1
0	8	NA	1.5–1.9	0	1	0
8	8	1	<0.1	0	2	2/3
8	8	2	1.3–1.7	0	2	2/3
8	8	2	1.3–1.5	0	2	2/3
ca. 8	ca.8	1	0.05	0	2	1
6–7	8	2	4.2–4.6	0	1	0
0	7–9	NA	0.15–0.25	0/1	1/2	1/2

abaxial cavities are often linear or linear-sinuate, but in some specimens are almost occluded by the strongly incurved wings (Fig. 5E). Both cypsela surfaces may be transversely rugose in both species, but more strongly in *A. perfoliata*. In *A. maidenii* sparse or moderately dense simple uniseriate trichomes to 60 μm long are present on the median abaxial wing and adaxial surface, and a tuft of glandular biseriate trichomes is present on the carpopodium between the abaxial wings. The cypselae are glabrous in *A. perfoliata*. The cypselae of *A. maidenii* are the longest (5–6 mm long) of any species examined.

SPECIES GROUP IX

Arctotis hirsuta (Fig. 6A, B)

Arctotis hirsuta is assigned to *A.* sect. *Hirsutae*. The cypselae are small (to 2.75 mm long) with 2 ovate-linear abaxial cavities, simple uniseriate trichomes, a coma is absent, and minute pappus scales are present. The apical plate is offset to the

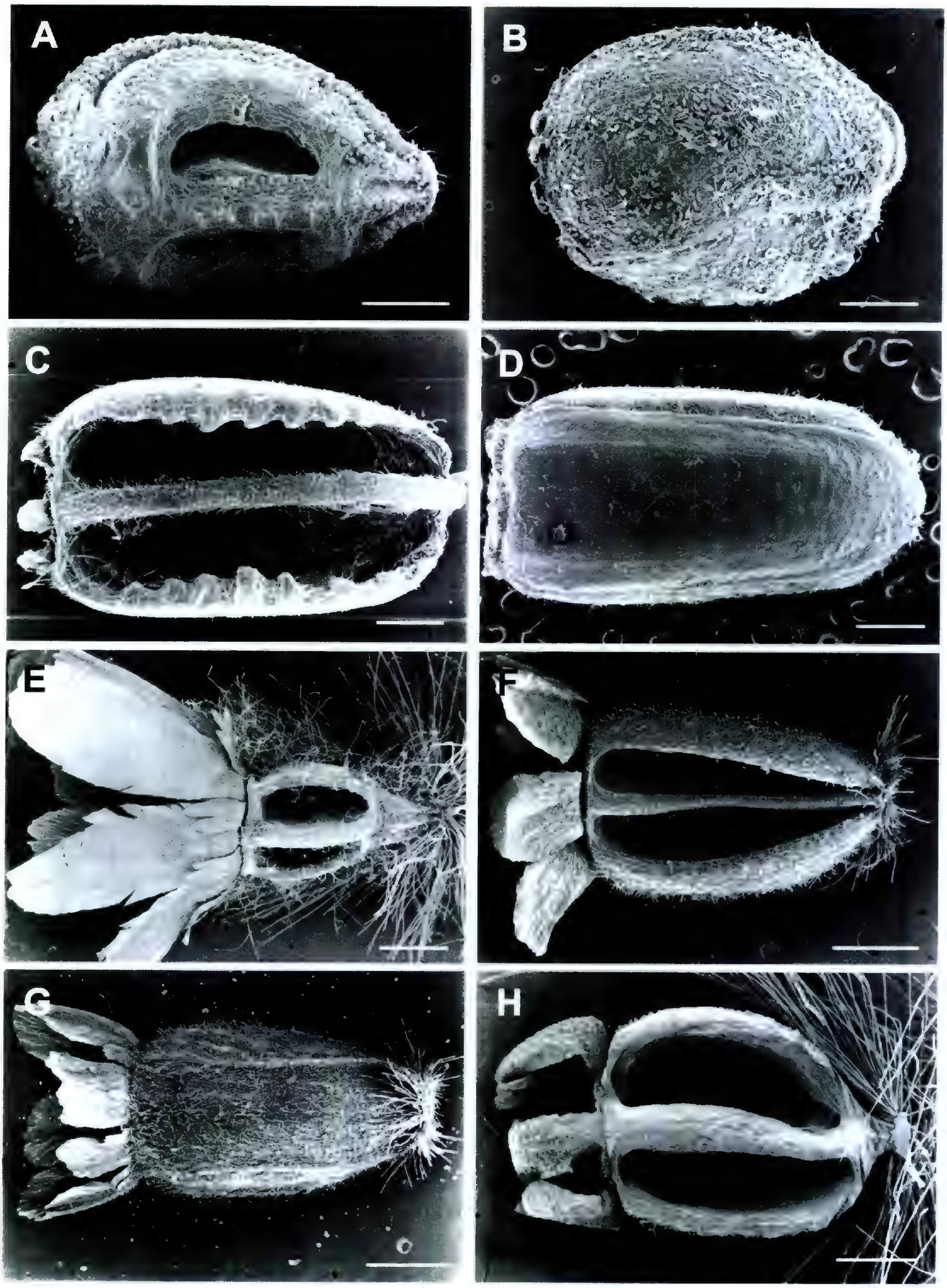

Figure 6. Cypselae of Arctotidinae. —A. *Arctotis hirsuta, N. S. Pillans 7693*, abaxial surface. Scale bar = 500 μm. —B. *A. hirsuta, N. S. Pillans 7693*, adaxial surface. Scale bar = 500 μm. —C. *Arctotis semipapposa, R. J. McKenzie 890*, abaxial surface. Scale bar = 500 μm. —D. *A. semipapposa, R. J. McKenzie 890*, adaxial surface. Scale bar = 500 μm. —E. *A. acaulis, R. J. McKenzie 848/1*, abaxial surface (trichomes partially removed). Scale bar = 1 mm. —F. *A. graminea, R. J. McKenzie 1084/2*, abaxial surface. Scale bar = 1 mm. —G. *A. graminea, R. J. McKenzie 1084/2*, adaxial surface. Scale bar = 1 mm. —H. *A. angustifolia, E. E. Esterhuysen 31373*, abaxial surface (coma partially removed). Scale bar = 1 mm.

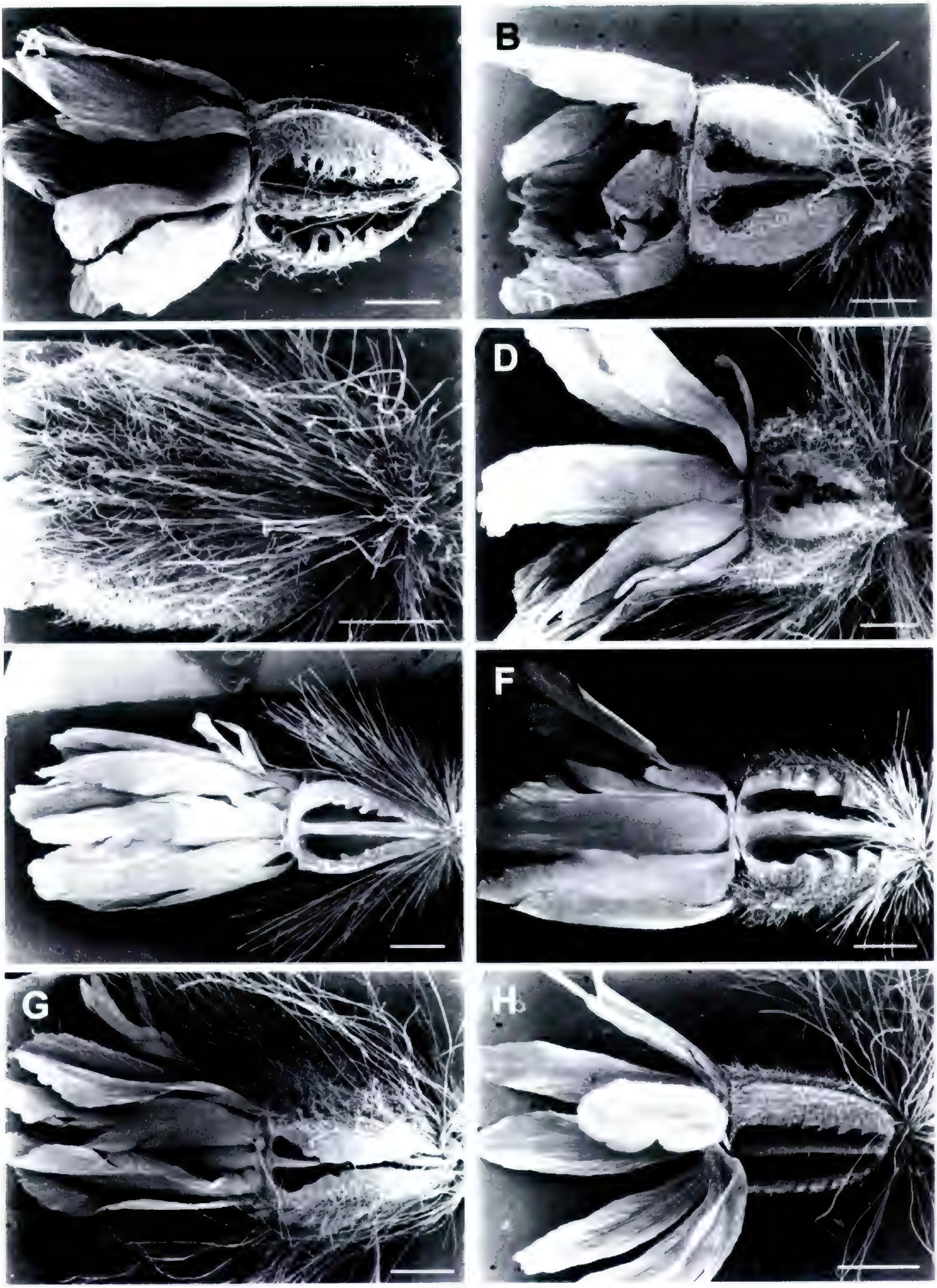

Figure 7. Cypselae of Arctotidinae. —A. *A. aspera* var. *aspera*, *R. J. McKenzie 847/1*, abaxial surface (trichomes removed). Scale bar = 1 mm. —B. *A. cuneata*, *R. J. McKenzie 826/1*, abaxial surface. Scale bar = 1 mm. —C. *A. cuneata*, *R. J. McKenzie 826/1*, adaxial surface. Scale bar = 1 mm. —D. *A. cuprea*, *R. Schlechter 8697*, abaxial surface (twin hairs and trichomes partially removed). Scale bar = 1 mm. —E. *A. gumbletonii*, *J. W. Matheus s.n.*, abaxial surface. Scale bar = 1 mm. —F. *A. rotundifolia*, *E. E. Esterhuysen 11129*, abaxial surface. Scale bar = 1 mm. —G. *A. scullyi*, *H. H. Bolus 9615*, abaxial surface. Scale bar = 1 mm. —H. *A. venusta*, *R. J. McKenzie 878/1*, abaxial surface. Scale bar = 1 mm.

abaxial side, and the cypsela has a strongly convex adaxial surface. The median abaxial wing is longer than the lateral abaxial wings. The cavities are rounded to obtuse at the apex and base. The 3 abaxial wings are fused in the lower part above the carpopodium. The base of the cypsela is short and constricted. The abaxial wings are entire or bear short, narrow, obtuse teeth; the wings are barely to strongly transversely rugose. The adaxial surface is always smooth. Clavate trichomes are sparse to moderately dense on the abaxial surface and dense on the adaxial surface. The cypselae have a uniseriate pappus of 8 or 9 rounded scales to 0.15 mm long, which are often longer on the adaxial surface.

SPECIES GROUP X

Arctotis semipapposa (Fig. 6C, D)

The species is placed in *Arctotis* sect. *Acuminatae*. The cypselae are obovate-cylindrical with a broad base, 3 abaxial wings forming 2 linear-sinuate cavities, and 2 adaxial ridges. The cypsela surface is smooth and bears sparse septate trichomes 100–135 μm long with an acute apex. The wings have short acute to rounded teeth. A coma of twin hairs is absent. Instead, glandular biseriate trichomes are usually present on the carpopodium, forming either a complete ring or tufts between the abaxial wings and adaxial ridges. The pappus is usually a single, incomplete whorl of 5 to 8 scales to 0.5 mm long. The scales are hemispherical with a rounded apex. The scales are longer on the abaxial side; adaxial scales are either rudimentary or absent. A partial outer whorl of rudimentary scales may be present on the abaxial side.

SPECIES GROUP XI

Arctotis acaulis (Fig. 6E), *A. verbascifolia*

The two species are placed in *Arctotis* sect. *Acaules* and *Adpressae* respectively. The cypselae are obconical-obovoid, with 3 abaxial wings and 2 adaxial ridges, the wings are fused in the lower part, the cypsela base is constricted into a short "stalk," septate trichomes and a coma of twin hairs are present, and the pappus of free scales is biseriate. The cypselar surface is smooth. The wings are entire or bear narrow, acute teeth on the lower half. The abaxial cavity is obovate or obovate-sinuate in *A. acaulis* and oblanceolate in *A. verbascifolia*. Septate trichomes are usually moderate to dense on the abaxial and adaxial surfaces. The coma exceeds the cypsela in length. Each pappus whorl consists of 8 scales. The outer whorl is much shorter than the inner whorl. The scales of the inner whorl are longest on the abaxial side, whereas the scales of the outer whorl are longest on the adaxial side. The scale apex is rounded in the inner whorl and obtuse in the outer whorl. The pappus exceeds the cypsela in length.

SPECIES GROUP XII

Arctotis graminea (Fig. 6F, G)

The species is assigned to *Arctotis* sect. *Revolutae*. The obconical-obovoid cypselae are distinguished by the reduced biseriate pappus, the short coma, and covering of short septate trichomes to about 300 μm long on all surfaces. Three abaxial wings and two adaxial ridges are present. The median abaxial wing is shorter than the lateral wings, which are entire and shortly inflexed. The abaxial cavity is linear-cuneiform. The cypselar surface is smooth. A short coma of twin hairs to 1 mm long (1/3 of the cypsela length) is present. Each pappus whorl consists of 8 scales with a rounded apex. The inner pappus whorl is up to 1.8 mm long (1/3 of the cypsela length); the scales of the outer whorl are rudimentary.

SPECIES GROUP XIII

Arctotis angustifolia (Fig. 6H), *A. argentea*, *A. aspera* var. *aspera* (Fig. 7A), *A. campanulata*, *A. cuneata* (Fig. 7B, C), *A. cuprea* (Fig. 7D), *A. gumbletonii* (Fig. 7E), *A. rotundifolia* (Fig. 7F), *A. scullyi* (Fig. 7G), *A. venusta* (Fig. 7H)

This species group comprises the remaining 11 *Arctotis* species examined. The species are assigned to seven sections: *Angustifoliae*, *Argentae*, *Asperae*, *Caudatae*, *Cuneatae*, *Revolutae*, and *Stoechadinae*. The cypselae are variably obconical with 3 well-developed abaxial wings and 2 adaxial ridges, septate trichomes are present on the cypsela surface, a coma of twin hairs is always present, and the pappus of scales is biseriate. The cypsela is obconical, obconical-obovoid or obconical-cylindrical in different species. The cypselar surface is smooth. The wings are entire or dentate; this may vary within a species. In some species the wings almost occlude the abaxial cavities (Fig. 7G). The median abaxial wing is shorter than, similar in length to, or longer than the lateral wings in different species. The abaxial cavity is either linear (*A. venusta*), linear-obovate (e.g., *A. angustifolia*), triangular-pandurate or linear-cuneiform. Apart from the coma, the cypselae may be entirely glabrous, as in *A. gumbletonii* (Fig. 7E). Usually septate trichomes are present on the cypsela surface; the density ranges from sparse to dense on both abaxial and

adaxial surfaces and may vary within a species (Table 2) and between the ray and disc florets. The terminal cell may be long, thread-like and interwoven with other trichomes to produce a woolly indumentum (Fig. 7C, G) or very reduced (less than 150 μm long) and not interwoven (e.g., *A. angustifolia*). In some species, such as *A. aspera* and *A. laevis*, the septate trichomes conceal the abaxial cavities. The coma consists of twin hairs varying in length from up to 1/3 the cypsela length to about 1.5 times the cypsela length. The coma is deciduous in *A. angustifolia* and persistent in the other species. The outer pappus whorl is much shorter than the inner whorl. In *A. angustifolia* the abaxial scales of the outer whorl may be reduced to tufts of minute bristles. The scales of the inner whorl are longest on the abaxial side, whereas the scales of the outer whorl are longest on the adaxial side. The scale apex is rounded in the inner whorl and obtuse in the outer whorl. The pappus length varies from slightly shorter than the cypsela length in *A. angustifolia* (Fig. 6H) to twice the cypsela length in *A. gumbletonii* (Fig. 7E).

Discussion

In examining the SEM micrographs, variable and notable features of the cypselae are apparent: longitudinal ridges or wings on the abaxial surface, the pappus scales, and surface features.

Abaxial Ridges or Wings

Cypselae of Arctotidinae present a progression from species with only weakly developed abaxial ridges (our Group I), through species with conspicuous abaxial ridges (Groups II–IV), to species with well-developed abaxial wings (Groups V–XIII). The number and extent of development of the abaxial ridges is constant within each species group with only few exceptions. The number of abaxial ridges is variable in *Arctotheca calendula* and *A. prostrata* (IV), and in *Arctotis microcephala* and *A. scapiformis* (VII) two to four adaxial ridges may be conspicuous. In *Haplocarpha oocephala* and *H. parvifolia* (II), the abaxial ribs are broad and separated by narrow furrows; in other species of Group II the ribs are narrow.

In *Arctotis* and *Cymbonotus* (V–XIII), two or three abaxial wings are developed that form either one or two cavities. The presence of the abaxial wings is a diagnostic feature of these genera; wings are more strongly developed in *Arctotis* (Bremer, 1994). Variation in development of the abaxial wings, shape of the cavities, and surface features (e.g., the presence of teeth and rugose ridges) affords means of distinguishing informal species groups. The median abaxial wing may be poorly developed so that only one cavity is obvious (e.g., *A. dregei* [V] and *A. fastuosa* [VII]). The lateral abaxial wings are less developed in Group VII than in Groups VIII–XIII. In *A. breviscapa* (VI) the two adaxial ridges are extended to form distinct wings; adaxial wings are also present, but less developed, in *A. dregei*. Lewin (1922a) emphasized this characteristic to distinguish *A.* sect. *Leptorhizae*; clearly, the presence of adaxial wings per se is not unique to *A. breviscapa*. Degree of inflexion of the lateral abaxial wings and development of the median abaxial wing are very different in *A. breviscapa* and *A. dregei* and are distinctive within *Arctotis*. In some species dentation of the abaxial wings is variable, particularly in length and shape, and is less helpful for delimiting species groups.

Outside of *Arctotis* and *Cymbonotus*, *H. lyrata* (II) is the only species in which the lateral abaxial ridges are curved toward the median abaxial ridge. This feature was noted also by Reese (1989). The lateral ridges are not well enough developed to be considered wings and do not create distinct collateral cavities as in *Arctotis* and *Cymbonotus*. This may represent either an early stage in the evolution of wings, or perhaps a past hybridization event with an *Arctotis* species. In other external cypsela features, *H. lyrata* is closely allied to *H. lanata* and, anatomically, the cypselae of *H. lyrata* are similar to *Arctotheca calendula*, *Arctotis*, and *C. lawsonianus* (Reese, 1989).

Pappus

The pappus is variable in Arctotidinae and is helpful to distinguish some species groups. When a pappus is present, it usually comprises unfused scales. A coronate pappus was observed in three species only (*Arctotheca populifolia* [IV], *Haplocarpha hastata* [I], and *H. schimperi* [III]), and in *A. populifolia* and *H. schimperi* the degree of fusion of the scales varies. A pappus of free scales is best developed in Groups II and XIII. The absence or extreme reduction of the pappus was used to support the segregation of *Landtia* from *Haplocarpha* (Phillips, 1951) and of *Venidium* from *Arctotis* (Lessing, 1832). The pappus is easily lost or reduced in some Compositae, so its form is not always a reliable generic criterion. The pappus is particularly variable in *Arctotheca* (IV—specimens may have no pappus, a single whorl of two to nine free scales, or a variably fused coronate pappus). The absence of even vestigial pappus scales is characteristic of most species in Groups VII and VIII, as

well as some specimens of *A. calendula* and *A. prostrata* (IV). Minute scales are characteristic of Group I, *Arctotis hirsuta* (IX), and some forms of *A. fastuosa* (VII). Previously, *Arctotis semipapposa* (X) was thought to be characterized by a very reduced uniseriate pappus comprising scales only on the abaxial side of the cypsela (Harvey, 1865); specimens examined in the present study indicate the number of scales is variable and that minute adaxial scales and a partial second whorl may also be present.

The scale apex shape is often variable within a species group and between the whorls on a single cypsela; acuminate apices are found only in *H. scaposa* and *H. lyrata* (II).

CYPSELA TRICHOMES

Cypselar pubescence was emphasized to support segregation of *Cryptostemma* and *Microstephium* from *Arctotheca* (e.g., Harvey, 1865; Bentham, 1873a, b); it was subsequently found to be untenable at the generic level (Lewin, 1922a). Pubescence density may vary between populations in *Arctotheca* and *Arctotis* species, even between ray and disc cypselae in the same capitulum in some *Arctotis* species; thus, it must be utilized cautiously as a taxonomic character.

Herman (2001) reported the presence of septate trichomes in four *Arctotheca* and three *Arctotis* species, and their absence in three *Haplocarpha* species. Our observations on a wider sample of species confirm their presence in *Arctotheca* (IV) and the "core" *Arctotis* group (XIII), and absence in *Cymbonotus* (VII) and *Haplocarpha* (I–III). The length of septate trichomes varies considerably among *Arctotis* species. Short septate trichomes (to 300 μm long) characterize the cypselae of *A. breviscapa* (VI), *A. graminea* (XII), and *A. semipapposa* (X); septate trichomes are typically much longer, thread-like, and interwoven to form a woolly indumentum in the "core" *Arctotis* group (XIII).

The presence of multicellular biseriate trichomes on cypselae of *Arctotheca calendula* (IV) was noted by Herman (2001). This trichome type was not observed in any other species. Herman stated these trichomes were interspersed among the septate trichomes; in specimens examined in the present study, multicellular biseriate trichomes were attached at the base of the cypsela only and thus may represent a coma. As indicated in Figure 2D, the multicellular biseriate trichomes are similar to the septate trichomes and require microscopic examination to distinguish. In all other Arctotidinae, the coma, when present, is composed of twin hairs.

Biseriate glandular trichomes are present on the carpopodium in Group VII and *A. semipapposa* (X), but rarely form a complete ring. These species lack a coma of twin hairs.

CORRELATION OF CYPSELAR MORPHOLOGY WITH TAXONOMY

Arctotheca

The four *Arctotheca* species studied form a closely knit and easily recognizable group (our Group IV) based on cypselar morphology. The cypselae are characterized by being bilaterally flattened with lateral ridges always well developed, wings absent, a coma of either twin hairs (*A. forbesiana, A. populifolia,* and *A. prostrata*) or multicellular biseriate trichomes (*A. calendula*), a moderate or dense covering of septate trichomes, and a pappus shorter than the cypsela (in some specimens the pappus is wanting). The sole species not studied, *A. marginata,* has narrowly elliptic, densely pilose cypselae bearing seven to ten narrowly elliptic, hyaline pappus scales with an acute apex (Beyers, 2002). In combination with its perennial, stoloniferous habit, this indicates *A. marginata* has a close affinity with *A. prostrata. Arctotheca* is well supported by other morphological characteristics, such as the possession of neuter ray florets, bisexual disc florets, and papillose filaments.

Cypselar pubescence and pappus structure have been used to discriminate *Arctotheca, Cryptostemma,* and *Microstephium* (e.g., Harvey, 1865; Bentham, 1873a, b; Beauverd, 1915). The reduced importance of these features as generic criteria in this group was recognized by Lewin (1922a). The present study highlights the variability of these features in *A. calendula* and *A. prostrata* and thus supports Lewin's (1922a) amalgamation of the three genera.

At least three distinct cypsela forms exist in *A. calendula* and *A. prostrata.* The cypselae of these two species vary in terms of the number of pappus scales present, number of prominent abaxial ridges, and the density of septate trichomes. According to previous authors, *A. prostrata* lacks a pappus (e.g., Candolle, 1837; Harvey, 1865; Lewin, 1922a; Goldblatt & Manning, 2000; Beyers 2002), or at most two pappus scales are present (Beauverd, 1915). In the present study, a pappus was absent in one specimen of *A. prostrata* examined (*P. A. Bean 2992* [BOL]) from the Touwsberg, Western Cape province. In other *A. prostrata* specimens examined, a uniseriate pappus of 7 to 9 scales was present. A single specimen of *A. calendula* examined (*J. Samuel 19* [GRA]) from the western Northern Cape province also lacked a pappus. This in-

dicates absence of a pappus is not a distinguishing characteristic of *A. prostrata*. The variation in cypselar morphology in *A. calendula* and *A. prostrata* indicates a reappraisal of their taxonomy is warranted. Both species also exhibit considerable variation in vegetative morphology (Harvey, 1865). *Arctotheca calendula* and *A. prostrata* can be discriminated on life form: *A. calendula* is a tufted annual, *A. prostrata* is perennial with prostrate, adventitiously rooting stems. Distinguishing them on reproductive morphology is less straightforward. Some forms of *A. calendula* from the Northern Cape province possess cypselae morphologically very similar to those of *A. prostrata* from the Eastern Cape province. A closer examination of geographical variation patterns, particularly of cypselar and involucral-bract morphology, is needed to clarify their circumscription.

Arctotheca populifolia cypselae are distinctive in the genus in their larger dimensions and coronate pappus. Intraspecific variation is mainly restricted to the number and extent of fusion of the pappus scales, as noted by Lewin (1922a). The pappus scales may be nearly completely separate or almost completely fused in cypselae from the same capitulum (Lewin 1922a). An additional potential source of variation is cryptic hybridization. A putative hybrid between *A. calendula* and *A. populifolia* from Maccassar Beach, Western Cape province (*C. Peter 84* [GRA]) has cypselae of intermediate dimensions with nine completely free pappus scales, intermediate pubescence, and an indistinct coma.

The cypselae of *A. forbesiana* are very similar to forms found in *A. calendula* and *A. prostrata*. Variability in this species is unknown, as only one specimen with mature cypselae was available for study.

Arctotis dregei (V) strongly resembles *Arctotheca calendula* in vegetative and floral morphology, and the two species are often confused in herbaria. The ray florets are neuter in both species and in corolla, filament, and style morphology *A. dregei* is barely distinguishable from *Arctotheca*. With respect to cypselar morphology, the affinities of *A. dregei* lie with *Arctotis*. A well-developed biseriate pappus of free scales, well-developed abaxial wings creating a distinct abaxial cavity, and a distinct coma of twin hairs are features shared among *A. dregei* and other *Arctotis* species.

Arctotis

On the basis of cypselar morphology *Arctotis* species assort to nine informal species groups herein. These generally correspond with 5 of Lewin's (1922a) 15 infrageneric sections, namely, sections *Acaules*, *Acuminatae*, *Anomalae*, *Hirsutae*, and *Leptorhizae*. The "core" *Arctotis* group (XIII) consists of species Lewin placed in the sections *Aequales*, *Angustifoliae*, *Argenteae*, *Asperae*, *Cuneatae*, and *Revolutae*. The cypselae in this group vary in terms of shape, pubescence, abaxial wing morphology, and, to a lesser extent, pappus and coma length. Other morphological features and molecular data are required to further elucidate relationships within this group. It is important to note that Lewin's sections were based on involucral bract and vegetative morphology, as well as cypselar morphology.

Cypselae of *A. verbascifolia* (XI), placed in section *Adpressae* by Lewin, have a close affinity with those of *A. acaulis*. Lewin distinguished section *Adpressae* by its absence of appendages on the outer involucral bracts. That character may vary among closely related taxa, as in the *A. arctotoides* species complex. Both sections *Acaules* and *Adpressae* are acaulescent or very shortly caulescent.

Arctotis graminea is distinctive and is known only from the Riversdale district, Western Cape province in South Africa. Lewin (1922a) placed it in section *Revolutae* and acknowledged not seeing mature cypselae when describing the species. Cypselar morphology indicates *A. graminea* is not close to *A. cuprea* and is misplaced in section *Revolutae*; its affinities are not clear at present.

Arctotis discolor and *A. perfoliata* (VIII) were placed in *A.* sect. *Austro-orientales* by Lewin (1922a). The cypselae differ from those of other species in having two well-developed abaxial wings and two cavities, rather than more weakly developed wings and a single cavity, suggesting an affinity with "core" *Arctotis* species (XIII). In overall morphology, *A. perfoliata* (including *A. discolor*) clearly has an affinity with the other species in section *Austro-orientales*, but cypselar morphology indicates it is somewhat isolated in the section.

For convenience, *Arctotis fastuosa* is herein grouped with species of *A.* sect. *Austro-orientales* and *Cymbonotus* (VII). However, at least three cypsela forms are distinguishable in *A. fastuosa*, and the resemblance of the cypselae may simply reflect convergence rather than a common ancestry. In two forms of *A. fastuosa* the cypselae bear very reduced pappus scales. In *Cymbonotus* and *A.* sect. *Austro-orientales* no specimen examined possesses cypselae with even vestigial pappus scales. However, the pappus could easily have been lost during the evolution of these groups. In one of these forms of *A. fastuosa* the cypselae have a concave abaxial surface and strongly convex adaxial surface, as in *A. hispidula* and *Cymbonotus lawsonianus*; the cyp-

selae are constricted and acute at the base and bear very reduced pappus scales in a single whorl. The latter characteristics are suggestive of *A. hirsuta* and present an alternative hypothesis of affinity. A third form of *A. fastuosa* has cypselae with very weakly developed abaxial wings and lacks a pappus. *Arctotis fastuosa* was previously placed in *Venidium* together with *A. hirsuta*, *A. semipapposa*, the species comprising *A.* sect. *Austro-orientales*, and taxa now included in these species (Lessing, 1832; Harvey, 1865; Stapf, 1928); after merging *Arctotis* and *Venidium*, Lewin (1922a) placed *A. fastuosa* in section *Caudatae* and *A. hirsuta* in section *Hirsutae*.

Cymbonotus

Possession of abaxial wings and collateral cavities on the cypsela is considered a diagnostic characteristic of *Arctotis* (Bremer, 1994). However, a close affinity between the cypselae of *Arctotis* sect. *Austro-orientales* (excluding *A. perfoliata*) and *Cymbonotus* is immediately apparent. On the basis of cypselar morphology, the two are inseparable and are assigned to Group VII. The lateral abaxial ribs are only moderately developed and strongly inflexed and form a single, linear or linear-sinuate cavity, the cypsela surface is often rugose with unicellular or uniseriate trichomes, the cypselae lack any trace of a pappus, a coma of twin hairs is absent, and glandular biseriate trichomes are often present on the carpopodium. *Cymbonotus* was published by Cassini (1825) and has been distinguished from *Arctotis* by the more weakly developed abaxial cypsela wings, absence of a pappus and a coma, and papillose filaments. *Venidium* was discriminated from *Arctotis* by the glabrous cypselae with weakly developed abaxial wings and devoid of a pappus (Lessing, 1831). Lessing (1832) accepted eight species in *Venidium*, but commented in a footnote (p. 29), "Nnm [sic] a praecedente [*Cymbonotus*] satis diversum?" Beauverd (1915) reduced *Cymbonotus* and *Venidium* to subgenera of *Arctotis* based on the similarities in cypselar morphology. Lewin (1922a) recognized *Cymbonotus*, but acknowledged that support from morphological evidence was weak and the main basis for its segregation was its geographical isolation. After seeing Beauverd's (1915) treatment, Lewin (1922b) concurred with Beauverd's classification of *Cymbonotus*. Subsequent authors (e.g., Norlindh, 1977; Murray, 1992; Bremer, 1994) continued to recognize *Cymbonotus* without comment on the close morphological similarity with species currently placed in *Arctotis* sect. *Austro-orientales*. As *Arctotis* is now circumscribed, cypselar morphology is clearly insufficient to support the independent segregation of taxa in *Cymbonotus* and *A.* sect. *Austro-orientales*. Filament ornamentation has also been used to support segregation of *Cymbonotus*, but on its own it may be an inadequate generic criterion in the Arctotidinae.

Arctotis maidenii was treated as *Cymbonotus* sp. 'A' by Murray (1992). Cypselar morphology implicates *A. maidenii* has a close affinity with *A. perfoliata* (both species placed in our Group VIII) rather than with either *Cymbonotus* species (placed in Group VII). However, the vegetative morphology of *A. perfoliata* and *A. maidenii* is quite different. *Arctotis perfoliata* is a sprawling decumbent perennial with ovate, subrotund or subcordate leaves 5–6.3 cm long (Harvey, 1865). *Arctotis maidenii* is an annual, multi-stemmed herb with lanceolate, pinnatifid leaves to 30 cm long (Beauverd, 1915; Murray, 1992). Additional sources of evidence are needed to further clarify the taxonomic affinities of *A. maidenii*.

Haplocarpha

Circumscription of *Haplocarpha* has been the subject of much contention. Cypselar morphology indicates it is an unnatural genus comprising three species groups (I, II, and III). These species groups partially support Beauverd's (1915) subgeneric groupings. Our Group I corresponds to *H.* subg. *Landtia* with the addition of *H. hastata* and exclusion of *H. schimperi*. Group II corresponds to *H.* subg. *Haplocarpha* with the addition of the recently transferred *H. oocephala* (Beyers, 2000). *Haplocarpha schimperi* (Group III) is indicated to be isolated in *Haplocarpha*.

Previously, three *Haplocarpha* species (*H. nervosa*, *H. rueppellii*, and *H. schimperi*) have been segregated in *Landtia* (Lessing, 1832; Harvey, 1865; Bentham, 1873a, b), but attempts to characterize *Landtia* by morphological criteria have proved unsatisfactory. *Haplocarpha* was published by Lessing (1831) and distinguished from other Arctotidinae by the presence of a uniseriate pappus of scales, scabrous filaments, pistillate ray florets, and absence of cypselar wings. Lessing (1832) distinguished *Landtia* from *Haplocarpha* primarily by its smooth filaments. However, the filaments are smooth in *H. parvifolia* (Lewin, 1922a). Additional characters discriminating *Haplocarpha* and *Landtia* have been proposed, such as pappus scale apex shape, cypsela shape, rugose versus smooth cypsela surface, pappus length relative to cypsela length, and lengths of peduncles relative to leaves (e.g.,

Harvey, 1865; Bentham, 1873a, b; Phillips, 1951). Closer scrutiny found them to be unsatisfactory and *Landtia* was merged with *Haplocarpha* (Beauverd, 1915; Lewin, 1922a). Beauverd (1915) concluded the distinction of pappus length relative to cypsela length and the presence of a median "vein" on the pappus scales were sufficient to distinguish *Landtia* as a subgenus of *Haplocarpha*.

Chromosome number and cypsela anatomy indicate *H. rueppellii* (I) has only a distant affinity with other Arctotidinae. *Haplocarpha rueppellii* has $2n = 30$ (Norlindh, 1977), in contrast to all other known chromosome counts in the Arctotidinae (including counts for *H. lyrata* and *H. scaposa*) of $2n = 18$ (e.g., Norlindh, 1977; Turner, 1970; Oberprieler & Vogt, 1993; Strother et al., 1996; Carr & King, 1999; Skinner, 2002). In this regard, *H. rueppellii* may have a distant affinity with *Gazania* and *Hirpicium* Cass. of the Gorteriinae, for which counts of $2n = 10$ and $2n = 20$ have been reported (Norlindh, 1977). In terms of cypsela anatomy, *H. rueppellii* possesses a cypsela form shared only with *H. scaposa*; *H. lyrata* cypselae are similar to those of *Arctotheca*, *Arctotis*, and *Cymbonotus* (Reese, 1989).

Cypselar morphology supports the transfer of *H. oocephala* (II) from *Arctotis* by Beyers (2000). The cypselae of *H. oocephala* are very similar to those of *H. parvifolia*, which is classified in *H.* subg. *Haplocarpha* (Beauverd, 1915), and lack the abaxial wings and cavities characteristic of *Arctotis*. *Haplocarpha* subg. *Haplocarpha* (including *H. oocephala*) forms a coherent group (II) characterized by cypselae with well-developed abaxial ridges, a pappus of free scales longer than the cypsela, and a coma of twin hairs at least equal in length to the cypsela. Distinctive features restricted to certain species in this group include shortly inflexed lateral ridges in *H. lyrata*, extremely broad abaxial ridges in *H. oocephala* and *H. parvifolia*, and acuminate pappus scale apices in *H. lyrata* and *H. scaposa*. The trichome type present on the cypsela surface varies in this group; long twin hairs exceeding the cypsela length cover the surface in *H. lanata* and *H. lyrata*, biseriate glandular trichomes are present on the abaxial ridges in *H. oocephala* and *H. parvifolia*, and the cypsela surface is glabrous in *H. scaposa*.

Cypselar morphology indicates *H. schimperi* (III) is not closely related to other species currently placed in *Haplocarpha*. The generic affinities of *H. schimperi* have long been uncertain. *Haplocarpha schimperi*, along with *H. rueppellii*, initially was placed in the specially erected genus *Schnittspahnia* Sch. Bip. (Schultz Bipontinus, 1842). Recognizing the morphological incongruence between the two species, Gay (1847) transferred *S. schimperi* Sch. Bip. to a new genus, *Ubiaea* J. Gay, before Bentham (1873a, b) merged both *Schnittspahnia* and *Ubiaea* with *Landtia*. Following the reduction of *Landtia* to a subgenus within *Haplocarpha* (Beauverd, 1915), *H. schimperi* still does not sit well in *Haplocarpha*. *Haplocarpha schimperi* is similar to subgenus *Landtia* in possessing a reduced pappus and lacking a coma, but differs in possessing well-developed, dentate abaxial ribs. From subgenus *Haplocarpha*, *H. schimperi* is distinguished by the reduced, sometimes coronate pappus, absence of a coma, and presence of uniseriate trichomes on the cypselae. Cypselar morphology suggests some affinity with *Arctotis fastuosa* and *Cymbonotus preissianus*, but *H. schimperi* differs from those species in consistently possessing a pappus and the abaxial ribs are not developed into wings.

Presence of well-developed abaxial ridges or wings on the cypsela is a possible synapomorphy of Arctotidinae (Funk et al., 2004). The weak development of the abaxial ribs in our Group I casts some doubt on this and indicates coding of this character requires some caution. Absence of conspicuous abaxial ridges or wings may be plesiomorphic in Arctotideae. Alternatively, a concomitant reduction of the abaxial ridges and pappus in Group I may be autapomorphic and would be consistent with the possession of geocarpic capitula in *H. nervosa* and *H. rueppellii* (Barker, 2005 this issue).

It is clear that a thorough reappraisal of other morphological characters and acquisition of molecular data is required to elucidate relationships among all *Haplocarpha* species and to clarify the generic circumscription.

Conclusions

This study confirms the utility of cypselar morphology for elucidating taxonomic relationships in Arctotidinae. *Arctotis* is indicated to comprise a large core group containing 11 of the species sampled; the other 14 species sampled are placed in eight different species groups. Lewin's infrageneric classification of *Arctotis* is partly supported, but additional morphological and molecular evidence is required to further resolve infrageneric relationships. *Arctotis* sect. *Austro-orientales* (excluding *A. perfoliata*) and *Cymbonotus* are indicated to have a close affinity, and an expanded *Cymbonotus* might be warranted. *Haplocarpha* is indicated to be an unnatural genus as circumscribed at present. Resurrection of *Landtia* is supported by cypselar mor-

phology. The affinities of *H. schimperi* are less certain; it seems misplaced in *Haplocarpha*. *Arctotheca* comprises a coherent group, but resolution of the circumscription of *A. calendula* and *A. prostrata* is required. Corroboration with other morphological characters and molecular data is still required for resolution of taxonomic relationships in Arctotidinae.

This study also highlights the importance of including as wide a sample of taxa as possible in initial investigations of taxonomic relationships. Selection of a too small sample of randomly selected representatives of genera, in the absence of knowledge of species groupings, may generate misleading relationships and conclusions, particularly regarding monophyly and delimitation of supraspecific taxa. Future investigations of Arctotidinae should include one or more representatives of *Haplocarpha* subg. *Landtia*, especially when studying the monophyly of the subtribe. The present study indicates five species (*Arctotis breviscapa*, *A. dregei*, *A. maidenii*, *A. perfoliata*, and *Haplocarpha schimperi*) are anomalous as classified at present and should be included in future phylogenetic studies to elucidate their relationships.

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Appendix 1. Cypselar Morphological Characters for Arctotidinae in Table 2.

1. *Cypsela shape:* (1) obconical; (2) obovoid to obovoid-cylindrical; (3) obovoid-elliptic; (4) obconical-obovoid; (5) obconical-cylindrical.
2. *Cypsela bilaterally flattened:* (0) absent; (1) present.
3. *Cypsela base constricted forming a short "stalk":* (0) absent; (1) present.
4. *Cypsela epidermis transversely rugose:* (0) absent; (1) abaxial surface/wings; (2) adaxial surface; (3) both surfaces.
5. *Median abaxial rib width:* (0) not very conspicuous; (1) narrow; (2) broad.
6. *Median abaxial rib transversely rugose:* (0) absent; (1) present.
7. *Median abaxial rib length v. lateral abaxial rib length:* (1) median rib shorter; (2) ± equal length; (3) median rib longer.
8. *Origin of cypsela wings:* (0) wings absent; (1) abaxial ribs only; (2) adaxial and abaxial ribs.
9. *Number of cavities formed by abaxial ribs.*
10. *Number of cavities formed by adaxial ribs.*
11. *Shape of abaxial cavity:* (1) obovoid; (2) linear; (3) linear-cuneiform; (4) triangular-pandurate; (5) pandurate-linear; (6) linear-ovate; (7) ovate.
12. *Cypsela wing margin:* (1) smooth; (2) dentate.
13. *Cypsela wing teeth apex:* (1) acute; (2) obtuse; (3) rounded; (4) truncate.
14. *Abaxial wing curvature toward median abaxial rib:* (1) weakly incurved; (2) moderately incurved; (3) abaxial cavities ± occluded by wings.
15. *Trichome type on cypsela epidermis:* (1) septate trichomes; (2) uniseriate trichomes with rounded apices; (3) twin hairs; (4) biseriate glandular trichomes; (5) narrow unicellular trichomes with acute apices; (6) clavate uniseriate trichomes.
16. *Trichome density on abaxial surface:* (0) glabrous; (1) sparse; (2) moderate; (3) dense.
17. *Trichome density on adaxial surface:* (0) glabrous; (1) sparse; (2) moderate; (3) dense.
18. *Trichomes on carpopodium:* (0) absent; (1) complete ring; (2) tuft/s on abaxial side only; (3) partial ring on adaxial side only.
19. *Maximum coma length v. cypsela length.*
20. *Coma trichome type:* (1) twin hairs; (2) multicelluar biseriate trichomes; (3) biseriate glandular trichomes.
21. *Trichomes on apical plate:* (0) absent; (1) present.
22. *Number of pappus series.*
23. *Number of pappus scales in outer series.*
24. *Number of pappus scales in inner series.*
25. *Relative length of pappus series:* (1) ± equal; (2) inner series at least double outer series.
26. *Pappus length v. cypsela length.*
27. *Pappus scale fusion:* (0) all scales free; (1) coronate.
28. *Pappus scale base:* (1) narrow; (2) broad.
29. *Pappus scale apex shape:* (0) acuminate; (1) acute; (2) obtuse; (3) rounded.

APPENDIX 2. Voucher details of specimens examined. The abbreviation of the herbarium where each specimen is lodged is in parentheses. Geographic abbreviations: EC = Eastern Cape, South Africa; ETH = Ethiopia; FS = Free State, South Africa; KZN = KwaZulu-Natal, South Africa; LES = Lesotho; NAM = Namibia; NC = Northern Cape, South Africa; NSW = New South Wales, Australia; SA = South Australia, Australia; TAS = Tasmania, Australia; VIC = Victoria, Australia; WC = Western Cape, South Africa. Collector abbreviations: JS = J. Samuel; NPB = N. P. Barker; RJM = R. J. McKenzie. Herbarium abbreviations: BOL = Bolus Herbarium; ETH = National Herbarium of Ethiopia; GRA = Selmar Schönland Herbarium; NBG = Compton Herbarium; NH = KwaZulu-Natal Herbarium; NSW = National Herbarium of New South Wales; PRE = Pretoria National Herbarium.

Taxa	Voucher specimens
Arctotheca calendula (L.) Levyns	EC, *Convent 40* (GRA); KZN, *C. J. Ward 5826* (PRE); KZN, *C. L. P. Zeyher s.n.* (GRA); WC, *C. Cottrell 7* (GRA); WC, *M. Francis* 11 (GRA); WC, *D. W. Gess* 91/92/3 (GRA); WC, *S. K. Gess, F. W. Gess & D. W. Gess* 89/90/38 (GRA); WC, *JS 16* (GRA); WC, *JS 19* (GRA); WC, *JS 37* (GRA); WC, *JS 45* (GRA); WC, *JS 48* (GRA); WC, *RJM 808/1* (GRA); WC, *RJM 1069/2* (GRA); WC, *R. Schlechter 8123* (GRA); WC, *W. C. Scully 30* (BOL).
Arctotheca calendula (L.) Levyns × *Arctotheca populifolia* (P. J. Bergius) Norl.	WC, *C. Peter* 84 (GRA).
Arctotheca forbesiana (DC.) K. Lewin	WC, *E. E. Esterhuysen 23126* (PRE).
Arctotheca populifolia (P. J. Bergius) Norl.	EC, *D. M. Comins 1041* (GRA); EC, *C. J. Cooper 32* (GRA); EC, *O. Hilmer 187* (GRA); EC, *C. Peter 211* (GRA); EC, *C. Peter 258* (GRA); EC, *G. Rattray 579* (GRA); WC, *RJM 771* (GRA); WC, *C. Peter 287* (GRA).
Arctotheca prostrata (Salisb.) Britten	EC, *H. H. Burrows 4679* (GRA); EC, *R. M. Cowling 338* (GRA); EC, *RJM 1129* (GRA); WC, *P. A. Bean 2992* (BOL); WC, *RJM 828* (GRA); WC, *RJM 829* (GRA); WC, *S. Schönland 3516* (GRA); WC, *A. J. Williamson 76* (GRA).
Arctotis acaulis L.	WC, *A. Hitchcock 924* (GRA); WC, *C. P. Immelman 1866/28* (BOL); WC, *RJM 848/1* (GRA); WC, *RJM 1030/3* (GRA); WC, *RJM 1041/3* (GRA); WC, *RJM 1047* (GRA); WC, *W. G. Welman 106* (PRE).
Arctotis angustifolia L.	WC, *L. Bolus s.n.* (BOL); WC, *E. E. Esterhuysen 31373* (NBG).
Arctotis arctotoides (L. f.) O. Hoffm.	EC, *RJM 724/1* (GRA); EC, *RJM 778/4* (GRA); EC, *RJM 781/2* (GRA); EC, *RJM 790/1* (GRA); EC, *RJM 793/1* (GRA); EC, *RJM 884/2* (GRA); EC, *RJM 887* (GRA); EC, *RJM 905/1* (GRA); EC, *RJM 908* (GRA); EC, *RJM 969/3* (GRA); FS, *Gray College Herb. 107* (BOL); KZN, *M. S. Evans 427* (NH); LES, *M. M. Page 15979* (BOL); LES, *M. D. Panagos 26* (NH).
Arctotis argentea Thunb.	WC, *E. E. Esterhuysen 29344* (BOL); WC, *E. E. Esterhuysen 29347* (BOL); WC, *H. C. Taylor 12022* (NBG); WC, *H. C. Taylor 1210,* (NBG); WC, *E. van Jaarsveld 12108* (PRE).
Arctotis aspera L. var. *aspera*	WC, *RJM 847/1* (GRA); WC, *RJM 895/1* (GRA).
Arctotis breviscapa Thunb.	WC, *C. Boucher & P. Shepherd 4602* (NBG, PRE); WC, *J. A. Marsh 1214* (NBG); WC, *F. A. Rogers 1062* (GRA); WC, *E. Werderman & H.-D. Oberdieck 473* (PRE).
Arctotis campanulata DC.	WC, *M. Lewis 19410* (BOL).
Arctotis cuneata DC.	EC, *NPB 1921* (GRA); EC, *R. A. Dyer 1686* (GRA); EC, *RJM 826/1* (GRA); EC, *M. J. Wells 2937* (GRA).
Arctotis cuprea Jacq.	WC, *R. Schlechter 8697* (BOL); WC, *W. G. Welman 29* (PRE).
Arctotis dregei Turcz.	EC, *H. H. Burrows 4639* (GRA); EC, *J. Burtt Davy 14245A* (BOL); EC, *RJM 1016/1* (GRA); EC, *P. Raal 1830* (GRA); NC, *J. Hutchinson 690* (BOL); WC, *K. Å. Dahlstrand 1445* (PRE); WC, *RJM 815/2* (GRA); WC, *RJM 833/2* (GRA); WC, *RJM 834/1* (GRA); WC, *RJM 1050/2* (GRA).
Arctotis fastuosa Jacq.	NAM, *Dinter 6063* (BOL); NAM, *H. Merxmüller & W. Giess 28462* (PRE); NC, *P. Burgoyne 1517* (PRE); NC, *R. H. Compton 11488* (NBG); NC, *B. Maguire 1907* (NBG); NC, *D. C. H. Plowes 7274* (PRE); NC, *M. F. Thompson 1066* (PRE); NC, *M. F. Thompson & A. le Roux 211* (NBG); WC, *S. M. Johnson 540* (NBG); WC, *H. H. W. Pearson 6558* (BOL).
Arctotis graminea K. Lewin	WC, *RJM 824/2* (GRA); WC, *RJM 1084/2* (GRA).
Arctotis gumbletonii Hook. f.	WC, *J. W. Mathews s.n.*, x.1931 (BOL).

APPENDIX 2. Continued.

Taxa	Voucher specimens
Arctotis hirsuta (Harv.) Beauverd	EC, *RJM 766*, ex cult. (GRA); WC, *RJM 1070/2* (GRA); WC, *N. S. Pillans 7693* (BOL); WC, *N. S. Pillans 8628* (BOL).
Arctotis hispidula (Less.) Beauverd	EC, *J. B. Gillett 2350* (NBG); EC, *RJM 760/1* (GRA).
Arctotis maidenii Beauverd	NSW, *W. E. Mulham s.n.*, viii.1971 (NSW); NSW, *W. E. Mulham 1145* (NSW); NSW, *T. & J. Whaite 3787* (NSW).
Arctotis microcephala (DC.) Beauverd	WC, *W. J. Hanekom 1963* (PRE).
Arctotis perfoliata (L. f.) O. Hoffm.	EC, *W. E. Dix 156* (NBG); WC, *E. E. Esterhuysen 31531* (BOL); WC, *H. G. Fourcade 64* (BOL); WC, *RJM 825/2* (GRA).
Arctotis rotundifolia K. Lewin	WC, *H. H. Bolus 1192* (BOL); WC, *E. E. Esterhuysen 11129* (BOL); WC, *R. Schlechter 9249* (BOL).
Arctotis scapiformis Thell.	EC, *A. White 41* (GRA); KZN, *T. A. Coleman 475* (NH).
Arctotis scullyi Dümmer	NC, *E. J. van Jaarsveld 7423*, (NBG); WC, *H. H. Bolus 9615*, (BOL).
Arctotis semipapposa (DC.) Beauverd	WC, *Gentry, Barclay & Van Bredá 18626* (PRE); WC, *RJM 890* (GRA); WC, *RJM 1178* (GRA).
Arctotis suffruticosa K. Lewin	EC, *R. Schlechter 2586* (BOL, GRA [isotypes]).
Arctotis venusta Norl.	EC, *J. E. Victor 1844* (GRA); FS, *H. H. Bolus s.n.*, ii.1904 (BOL); FS, *RJM 873/1* (GRA); FS, *RJM 878/1* (GRA); WC, *Kitto s.n.*, ex cult., x.1931 (BOL).
Arctotis verbascifolia Harv.	WC, *E. G. H. Oliver 3951* (NBG).
Cymbonotus lawsonianus Gaudich.	NSW, *J. L. Boorman s.n.*, xii.1916 (NSW); NSW, *R. Coveny 8772* (NSW); NSW, *R. Coveny 10217* (NSW); NSW, *R. Coveny 7406, D. Benson & H. Bryant* (NSW); NSW, *J. M. Dalby 86/128* (NSW); NSW, *G. L. Davis s.n.*, 16.1.1941 (NSW); NSW, *K. Mair s.n.*, 20.x.1957 (NSW); NSW, *E. J. McBarron 14438* (NSW); NSW, *S. McIntyre 5-8* (NSW); NSW, *J. Pickard 296 & D. Blaxell* (NSW).
Cymbonotus preissianus Steetz	NSW, *E. F. Constable s.n.*, 25.x.1958 (NSW); NSW, *R. Coveny 10773 & J. Armstrong* (NSW); NSW, *A. Rodd 1606* (NSW); NSW, *H. Salasoo 2113* (NSW); SA, *D. N. Kraehenbuehl 4835* (PRE); TAS, *R. C. Gunn 509* (NSW); VIC, *S. G. Hannaford s.n.*, viii.1853 (NSW); VIC, *J. R. Hosking 49* (NSW).
Haplocarpha hastata K. Lewin	ETH, *J. W. Ash 1700* (ETH); ETH, *O. Hedberg 5698* (ETH).
Haplocarpha lanata Less.	WC, *F. J. Kruger 441* (PRE).
Haplocarpha lyrata Harv.	EC, *RJM 1116* (GRA).
Haplocarpha nervosa (Thunb.) Beauverd	EC, *R. A. Dyer 786* (GRA); EC, *RJM 1125/1* (GRA).
Haplocarpha oocephala (DC.) Beyers	WC, *E. E. Esterhuysen 34661* (BOL).
Haplocarpha parvifolia (Schltr.) Beauverd	WC, *E. E. Esterhuysen 36048* (PRE).
Haplocarpha rueppellii (Sch. Bip.) Beauverd	ETH, *M. Thulin, A. Hunde & M. Tadesse 3715* (ETH).
Haplocarpha scaposa Harv.	EC, *RJM 909/4* (GRA).
Haplocarpha schimperi (Sch. Bip.) Beauverd	ETH, *NPB 1899* (GRA, ETH); ETH, *S. H/Manam 1* (ETH); ETH, *M. Thulin 1609* (ETH).

ANÁLISIS DE LA DIVERSIDAD Y DISTRIBUCIÓN GEOGRÁFICA DE LA FAMILIA POACEAE EN LA PROVINCIA DE JUJUY, ARGENTINA[1]

Osvaldo Morrone,[2] Sandra S. Aliscioni,[3] y Fernando O. Zuloaga[2]

Resumen

En este trabajo se presenta una actualización del conocimiento de la diversidad de Poaceae en la provincia de Jujuy. Se analiza la riqueza a nivel de subfamilia, tribu, género, especie, subespecie y variedad. Se registraron 373 especies y 23 taxones infraespecíficos, distribuidos en 91 géneros de Poaceae. Se analiza la distribución geográfica de los taxones por departamento, provincia fitogeográfica y rango altitudinal. Asimismo, se discuten las afinidades florísticas con otras áreas del país y de países limítrofes, y se mencionan taxones endémicos, los cuales sumaron un total de 10 especies y 2 variedades para la provincia.

Abstract

This study presents the current knowledge of diversity of the Poaceae family in the province of Jujuy, Argentina. Richness was analyzed at the following levels: subfamily, tribe, genus, species, subspecies, and variety. A total of 91 genera, 373 species, and 23 infraspecific taxa of Poaceae were found in the province. The geographic distribution of the taxa by department, phytogeographic province, and altitudinal range was analyzed. Affinities of the Poaceae of Jujuy with other regions of the country, and neighboring countries, are also discussed. In addition, a total of 10 species and 2 varieties were found to be endemic in the province.

Key words: Argentina, biodiversity, geographical distribution, Jujuy, Poaceae.

El Noroeste de la República Argentina (NOA) se caracteriza por una marcada heterogeneidad de paisajes, producto de los diversos factores orográficos y climatológicos presentes en la zona. En particular, la provincia de Jujuy se distingue por su diversidad de ambientes y regiones fitogeográficas, lo cual se manifiesta en su abundante flora (Cabrera, 1957; Vervoorst, 1979, 1982). Es una de las áreas del país con mayor riqueza específica de plantas vasculares, donde están representadas 170 familias, 972 géneros y 2831 especies (Zuloaga et al., 1999). En relación a la familia Poaceae, Zuloaga et al. (1999) señalan la presencia de 315 especies para la provincia, siendo luego de las Asteraceae (488 especies), la segunda familia mejor representada.

Jujuy se ubica como una cuña en el noroeste Argentino, situada entre los paralelos de 21°47′–24°37′ de latitud sur y los meridianos 64°09′–67°19′ de longitud oeste, abarcando un área de 53 219 km². La provincia limita al norte y al noroeste con la República de Bolivia, al este y al sur con la provincia de Salta y al oeste con la República de Chile. Se halla dividida políticamente en 15 departamentos provinciales: Dr. Manuel Belgrano (BEL), Cochinoca (COC), El Carmen (ECA), Humahuaca (HUM), Ledesma (LED), Rinconada (RIN), San Antonio (SAN), Santa Bárbara (SBA),

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[2] Instituto de Botánica Darwinion, Labardén 200, Casilla de Correo 22, San Isidro B1642HYD, Argentina. omorrone@darwin.edu.ar.

[3] Cátedra de Botánica Agrícola, Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, C1417DSE, Buenos Aires, Argentina.

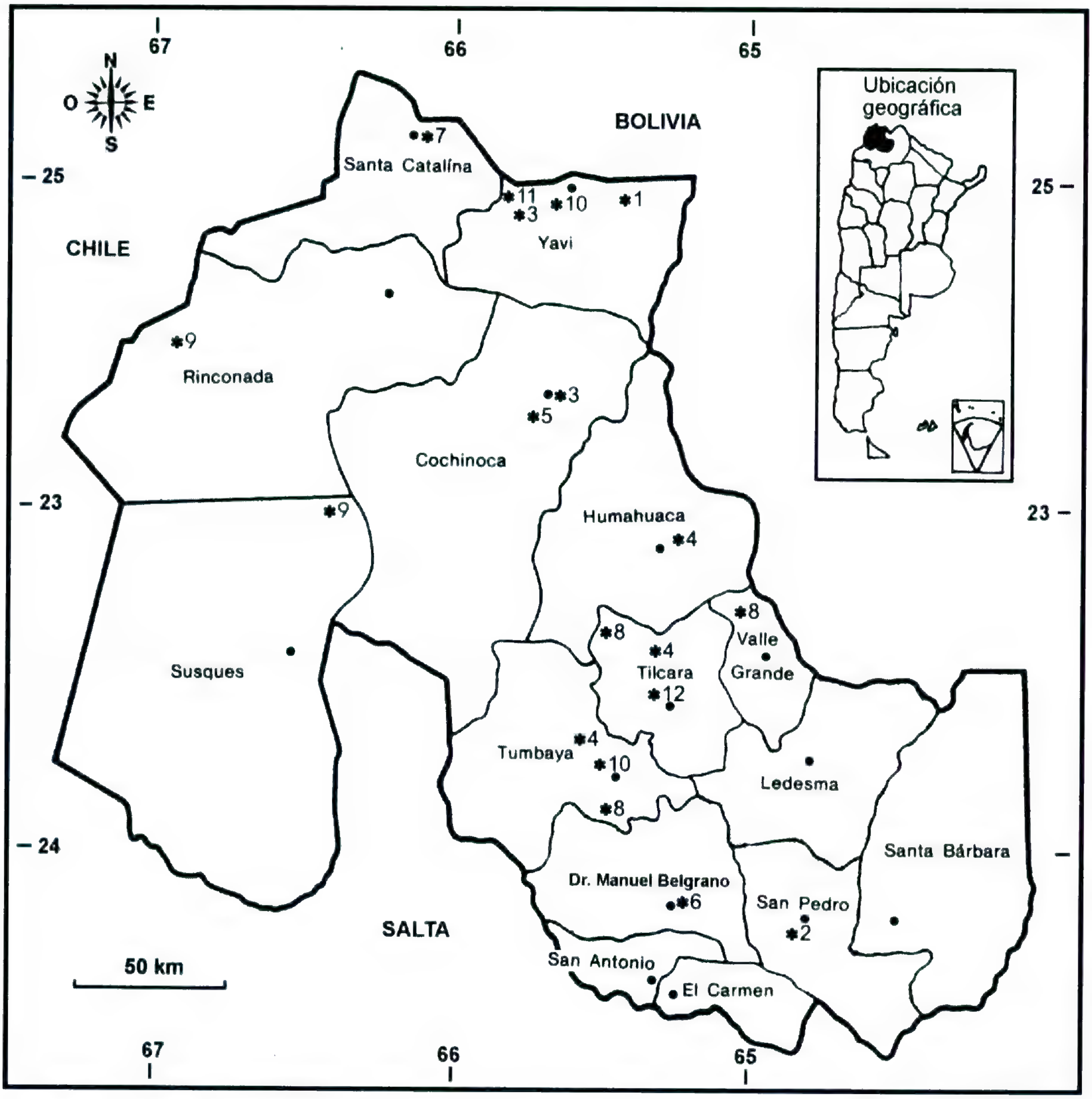

Figura 1. Mapa de la provincia de Jujuy con las divisiones políticas y la distribución de los taxones endémicos. (●) Ciudad cabecera de Departamento. (★) Taxón endémico: 1. *Aristida amplexifolia*; 2. *Aristida pedroensis*; 3. *Aristida pubescens*; 4. *Eragrostis andicola*; 5. *Deyeuxia cabrerae* var. *maxima*; 6. *Festuca superba*; 7. *Poa grisebachii*; 8. *Anatherostipa brevis*; 9. *Anatherostipa henrardiana*; 10. *Nassella pubiflora* var. *levipoda*; 11. *Nassella yaviensis*; 12. *Elymus tilcarensis*.

Santa Catalina (SCA), San Pedro (SPE), Susques (SUS), Tilcara (TIL), Tumbaya (TUM), Valle Grande (VGR) y Yavi (YAV) (Fig. 1).

La provincia ocupa una posición recostada casi totalmente sobre las estribaciones Andinas. Los cordones montañosos encierran numerosos valles y quebradas cubiertos por material sedimentario donde se han asentado poblaciones humanas, hallándose estos asentamientos entre los 300 y casi los 4000 m s.m.

El paisaje predominante está caracterizado por altiplanicies, montañas andinas y subandinas que abarcan aproximadamente el 75% de la superficie total, con una altura media superior a los 3500 m s.m. Hacia el norte y el oeste se presenta una extensa meseta, con algunas lagunas, las cuales son cuencas de drenaje cercadas por sierras. Las sierras de Santa Victoria y del Aguilar representan el límite oriental de esta árida penillanura. El resto del territorio son valles, llanuras y formaciones submontañosas, que se encuentran principalmente por debajo de los 1300 m s.m. (Braun Wilke et al., 2001).

De acuerdo con Hueck (1978), Jujuy presenta en la zona occidental una vegetación andina de alta montaña, tipo Puna, y hacia la zona oriental

bosques secos y mesofíticos. Entre ambas formaciones, se hallan intercalados parches de pluviselva andina y de bosques andinos perennes y deciduos, que llegan desde Bolivia y se extienden hasta Tucumán, atravesando el territorio jujeño.

El clima varía notablemente con la altitud y las direcciones de las sierras, quebradas y valles. Sobre la base de estas características geográficas pueden diferenciarse zonas climáticas que varían de noroeste a sureste de la provincia, con amplias zonas de clima frío y seco en el sector puneño, hasta sectores con temperaturas tropicales e intensas lluvias. El régimen de lluvias es de tipo monzónico, donde las regiones más secas corresponden a las zonas de montañas altas donde los registros pluviométricos son comparativamente menores que los presentes en las regiones bajas (De Fina, 1992).

En la provincia se establecen fundamentalmente tres tipos de clima (Buitrago & Larran, 1994): a—En la zona de la Puna por encima de los 3000 m s.m., se presenta el clima Andino Puneño caracterizado por su manifiesta aridez, con registros de temperaturas de hasta 30°C durante el día, producto de la gran insolación, y con bruscos descensos nocturnos por debajo de 0°C. El régimen de lluvias varía entre 250 a 400 mm anuales, concentrados desde mediados de noviembre a marzo. En los sectores más altos de esta zona, las precipitaciones en forma de nieve y granizo adquieren relevancia. b—Siguiendo en dirección noroeste a sureste, hacia la zona de los valles, el clima es subtropical con estación seca, caracterizado por altas temperaturas en verano, las que coinciden con el período de lluvias. En esta época del año se registran temperaturas elevadas, superiores a los 40°C, y las lluvias de régimen monzónico, varían entre los 400 y 1500 mm anuales. c—En la zona sureste el clima es templado y subtropical serrano, con lluvias de tipo monzónico y una variación en el promedio anual entre 500 y 1500 mm. La temperatura media mensual de enero (verano) es de 21°C y en julio (invierno) ésta desciende a 10.5°C.

Desde el punto de vista biogeográfico, el territorio se halla comprendido dentro de la Región Neotropical, incluyendo tres Dominios y cinco provincias fitogeográficas: dentro del Dominio Amazónico, la Provincia de las Yungas (YUN); dentro del Dominio Chaqueño, las Provincias Chaqueña (CHA) y de la Prepuna (PRE); y dentro del Dominio Andino-Patagónico, las Provincias Puneña (PUN) y Altoandina (ALT) (Cabrera & Willink, 1973; Cabrera, 1976) (Fig. 2).

La Provincia de las Yungas (YUN) se extiende por las laderas orientales de los Andes, desde Venezuela hasta el noroeste de Argentina, aproximadamente desde los 500 a 2500 o 3500 m s.m. según la latitud. Se caracteriza por un clima cálido y muy húmedo con lluvias estivales, y la presencia de neblina cubriendo casi continuamente las montañas; la precipitación anual varía de 900 a 2500 mm y la temperatura media entre los 14°C y 26°C, aunque ambas disminuyen a medida que aumenta la altura. La vegetación que predomina es la selva nublada rica en árboles de las familias Lauraceae y Myrtaceae, abundantes lianas y epífitos, y un estrato denso de hierbas y arbustos (Cabrera & Willink, 1973).

La Provincia Chaqueña (CHA) se localiza desde el sur de Bolivia y oeste de Paraguay hasta el centro de Argentina, cubriendo llanuras y serranías de escasa elevación, con un clima continental. La temperatura media anual es de 20°C a 23°C y las lluvias son estivales, con alrededor de 500 mm anuales de precipitaciones. La vegetación predominante es el bosque xerófilo caducifolio con estrato herbáceo de Poaceae y numerosas Cactaceae y Bromeliaceae; también se hallan en esta provincia sabanas y estepas arbustivas halófitas (Cabrera & Willink, 1973).

La Provincia de la Prepuna (PRE) se encuentra en las laderas y quebradas del sur de Bolivia y noroeste de Argentina, en este último país desde Jujuy a la provincia de La Rioja, entre los 2000 y 3400 m s.m. El clima es seco y cálido con lluvias exclusivamente estivales, la vegetación dominante es la estepa arbustiva xerófila baja y esparcida, mezclada con Cactaceae arborescentes, con dominancia del género *Trichocereus* (A. Berger) Riccob.; en las depresiones y orillas de los ríos se observan bosques bajos de *Prosopis ferox* Griseb. y matorrales de *Schinus areira* L. y *Baccharis salicifolia* (Ruiz & Pav.) Pers.; también hay Bromeliaceae que forman cojines (Cabrera & Willink, 1973).

La Provincia Puneña (PUN) se encuentra en el altiplano constituido por bolsones llanos dispuestos entre los dos brazos de la cordillera de los Andes, los que se abren entre los paralelos 15°S y 27°S. La altitud en esta región varía entre los 3200 a 4400 m s.m., los suelos son inmaduros, el clima es seco y frío con temperaturas medias de 8°C a 9°C, las lluvias son estivales, con alrededor de 50 a 700 mm anuales, disminuyendo de este a oeste. La composición de la vegetación es bastante uniforme, predomina la estepa arbustiva la cual se empobrece paulatinamente hacia la zona más seca. En los suelos más húmedos hay pastizales y bosques abiertos de *Polylepis tomentella* Wedd.

La Provincia Altoandina (ALT) abarca las altas montañas de Los Andes, desde Venezuela hasta Tierra del Fuego; la altitud a la que se encuentra varía

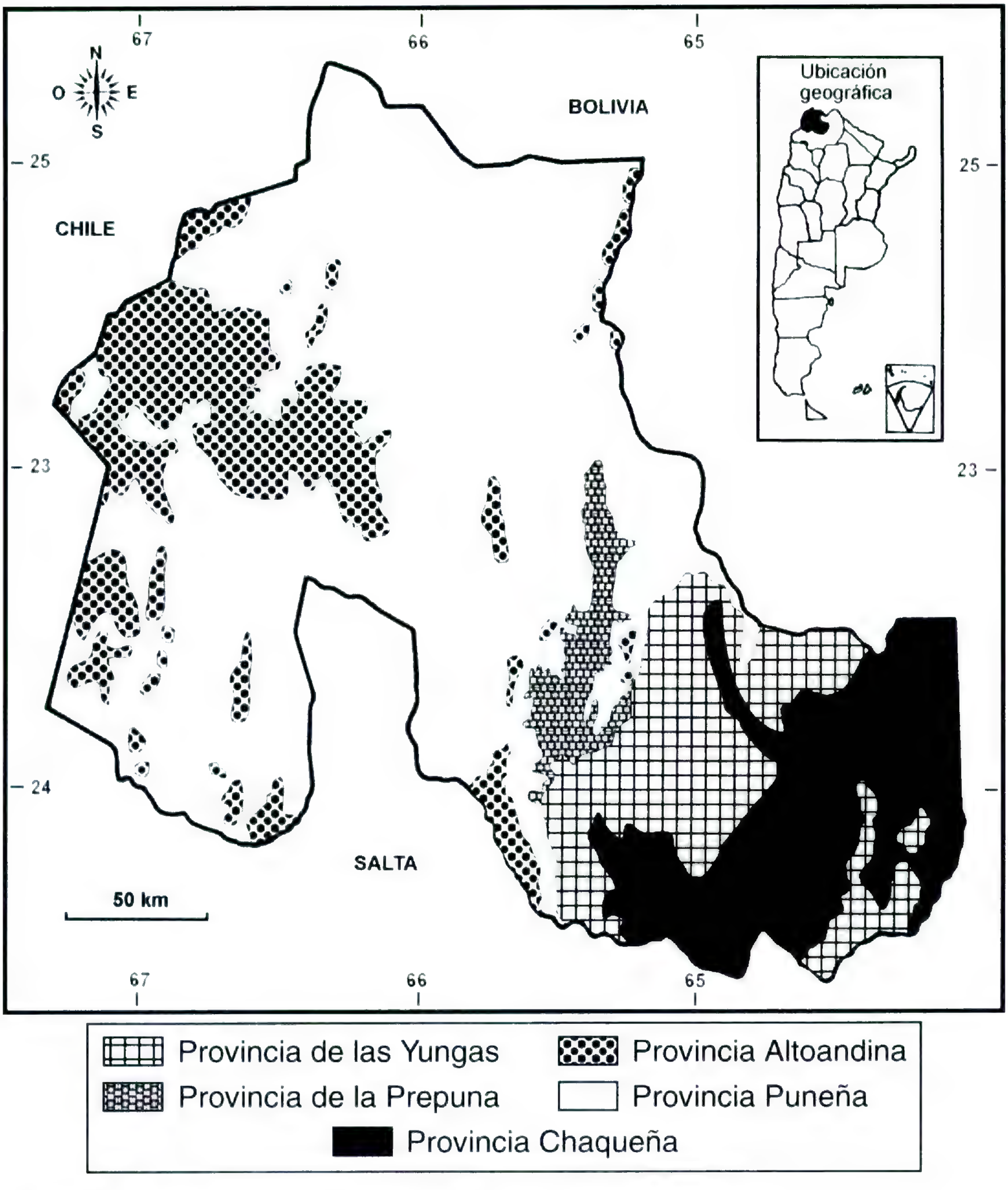

Figura 2. Mapa de las Provincias Fitogeográficas de Jujuy.

con la latitud: en Jujuy esta provincia biogeográfica se halla por encima de los 4400 m s.m. y se caracteriza por sus suelos inmaduros, sueltos, rocosos o arenosos. El clima es de alta montaña, frío y seco, con precipitaciones en forma de nieve o granizo y temperatura media por debajo de los 8°C. La vegetación es escasa, principalmente formada por estepas graminosas y caméfitas en cojín (Cabrera & Willink, 1973).

En lo referente al nivel de conservación, Jujuy cuenta con áreas protegidas dada su significativa biodiversidad tanto en flora como en fauna. Según el Sistema de Áreas Protegidas de Argentina (SIFAP ⟨http://www.medioambiente.gov.ar/sian/default.htm⟩) perteneciente a la Secretaría de Ambiente y Desarrollo Sustentable de la Nación, la provincia de Jujuy posee dos áreas protegidas bajo jurisdicción nacional: Parque Nacional Calilegua y Monumento Nacional Laguna de Los Pozuelos, y seis de jurisdicción provincial: Parque Provincial Potre-

ro de Yala, Monumento Natural Laguna Leandro, Reserva Provincial Alto Andina de la Chinchilla, Reserva de Fauna y Flora Olaroz-Cauchari, Reservas de la Biósfera Yungas-2 y Laguna de Los Pozuelos; las dos últimas tienen categoría internacional. En total estas áreas suman aproximadamente 10650 km^2, cerca del 20% de la superficie total de la provincia. No obstante debe destacarse que el grado de control en estas áreas es, a menudo, insuficiente o prácticamente nulo.

El objetivo básico del presente estudio es actualizar el conocimiento sobre la diversidad de especies de Poaceae en la provincia de Jujuy. Para ello se analiza el principal componente de la diversidad que es la riqueza específica. Se presenta una lista crítica de especies, se describen patrones de distribución geográfica, altitudinal, y fitogeográfica, y se discuten las afinidades florísticas con otras áreas de la República Argentina y con los países limítrofes (Bolivia y Chile). Asimismo, se discuten las preferencias ecológicas de las diferentes subfamilias de Poaceae, la relación de las subfamilias con las diferentes regiones biogeográficas, un análisis de la flora de regiones de los países limítrofes, y una comparación de número de endémicos en relación a otras familias de plantas vasculares.

Materiales y Métodos

La información sobre los registros de las especies fue ingresada a una base de datos de Poaceae (IRIS©) y fue compilada con: 1—información proveniente de exploración de campo y colección de especímenes botánicos realizada por los autores entre los años 1997–2000; 2—estudio de especímenes botánicos depositados en los herbarios BAA, LIL, LP, MO y SI; y 3—consulta de la bibliografía disponible (Anton & Hunziker, 1978; Gould, 1980; Gutiérrez & Pensiero, 1998; Judziewicz et al., 2000; Nicora, 1995, 1998; Pensiero, 1986, 1999; Peterson & Annable, 1991, 1992; Peterson et al., 2001; Renvoize, 1998; Rúgolo de Agrasar, 1974, 1994, 1995; Rúgolo de Agrasar & Molina, 1992; Rúgolo de Agrasar & Villavicencio, 1995; Sulekic & Zapater, 2001; Torres, 1997a–c). Cabe destacar, que se consultaron las extensas colecciones realizadas en Jujuy por A. L. Cabrera y H. Fabris (depositadas en LP y SI). La información sobre los especímenes estudiados, que incluyen datos sobre lugar de colección, fechas y herbario, se encuentra disponible en la pagina Web del Instituto Darwinion (⟨www.darwin.edu.ar⟩).

En la Tabla 1 se da una lista con las especies encontradas en la región, con un ejemplar de referencia y el acrónimo correspondiente al herbario de acuerdo con Holmgren et al. (1990), el departamento y la provincia fitogeográfica en donde se encontró, el rango de distribución altitudinal, el número de colecciones estudiadas y el ciclo de vida. Las coordenadas geográficas de las localidades fueron tomadas directamente de las etiquetas de los ejemplares de herbario, en los casos en donde la información era faltante la localidad fue georeferenciada empleando el Atlas de la República Argentina (Instituto Geográfico Militar-Ejercito Argentino) o el "Worldwide Index" (⟨www.tago.com⟩).

En relación a los factores ambientales, se consideró solamente el rango altitudinal, ya que la información sobre otros factores, como los climáticos, es muy restringida en la provincia, sólo se cuenta con tres estaciones meteorológicas en San Salvador de Jujuy (Dr. M. Belgrano), Abra Pampa (Cochinoca) y La Quiaca (Yavi).

Los taxones fueron agrupados en subfamilias y dentro de cada una de ellas en tribus siguiendo el criterio aceptado por Grass Phylogeny Working Group (GPWG, 2001) y Catalogue of New World Grasses (Poaceae) (Judziewicz et al., 2000; Peterson et al., 2001). Para los nombres de las especies se usó básicamente la obra de Zuloaga et al. (1994), más algunos cambios genéricos y específicos propuestos en los últimos años para las Poaceae.

Para evaluar la calidad de los datos obtenidos, en relación al número de especies registradas por departamento, se calculó el Índice de Chao (1984), el cual permite estimar la riqueza específica principalmente en áreas que han sido poco muestreadas o de las cuales se sospecha no contar con la totalidad de los registros. Para calcular el número de especies estimado por departamento se aplicó la siguiente fórmula: $S_{estimado} = S_o + (a^2/2b)$ donde S_o representa el número de especies observadas, a es el número de especies registradas una sola vez y b es el número de especies registradas dos o más veces. Los taxones infraespecíficos no fueron considerados para el cálculo del mencionado índice.

La similitud específica a nivel de departamentos y de provincias fitogeográficas fue calculada utilizando el coeficiente de similitud de Sørensen ($C = 2a/[b + c]$) donde a es el número de especies compartidas por las dos áreas comparadas y b y c son los números de especies solamente presentes en la primera y en la segunda de las áreas, respectivamente. Este coeficiente se empleó en el análisis de agrupamiento utilizando técnicas de ligamiento promedio ponderado (UPGMA), que fue llevado a cabo con el software NTSYS-pc (Numerical Taxonomy System of Multivariate Statistical Programs, Rohlf, 1998).

Tabla 1. Lista de las especies registradas de Poaceae de la provincia de Jujuy con datos de altitud, distribución por departamentos y por provincias fitogeográficas en Jujuy, número de colecciones observadas (#), ejemplar de referencia seleccionado (para referencias de los acrónimos véase materiales y métodos) y ciclo de vida (A = anual, P = perenne). * taxón endémico; ** taxones restringidos; [1] taxones introducidos. Provincias fitogeográficas: Provincia Altoandina (ALT), Provincia Chaqueña (CHA), Provincia de la Prepuna (PRE), Provincia Puneña (PUN) y Provincia de las Yungas (YUN). Departamentos: Dr. Manuel Belgrano (BEL), Cochinoca (COC), El Carmen (ECA), Humahuaca (HUM), Ledesma (LED), Rinconada (RIN), San Antonio (SAN), Santa Bárbara (SBA), Santa Catalina (SCA), San Pedro (SPE), Susques (SUS), Tilcara (TIL), Tumbaya (TUM), Valle Grande (VGR), Yavi (YAV).

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Subfamilia Aristidoideae						
Tribu Aristideae						
Aristida adscensionis L.	2900–3990	ALT, PRE, PUN	HUM	*Zuloaga 5908* (MO, SI)	2	A
			RIN	*Zuloaga 6020* (MO, SI)		
Aristida amplexifolia Caro & E. A. Sánchez*	3600	PUN	YAV	*Cabrera 9483* (LP)	2	P
Aristida asplundii Henrard**	3400–3442	PUN	COC	*Cabrera 7745* p.p. (LP)	3	P
			YAV	*Parodi 9633* (BAA)		
Aristida enodis Hack.**	2800–3500	PRE, PUN	COC	*Cabrera 9430* (LP)	3	P
			TUM	*Cabrera 18411* (LP)		
			VGR	*Fabris 5843* (LP)		
Aristida pedroensis Henrard*	600	CHA	SPE	*Parodi 9784* (BAA)	1	P
Aristida pubescens Caro & E. A. Sánchez*	3500	PUN	COC	*Cabrera 7745* p.p. (LP)	2	P
			YAV	*Ruthsatz 250/2* (BAA)		
Subfamilia Arundinoideae						
Tribu Arundineae						
Phragmites australis (Cav.) Trin. ex Steud.	2190–2200	PRE	TIL	*Budin 35* (LIL)	1	P
			TUM	*Cabrera 31555* (SI)		
Subfamilia Bambusoideae						
Tribu Bambuseae						
Chusquea lorentziana Griseb.	1600–1700	YUN	BEL	*Deginani 187* (SI)	2	P
Tribu Olyreae						
Olyra fasciculata Trin.	600	YUN	LED	*Iudica 376* (SI)	1	P
Subfamilia Chloridoideae						
Tribu Cynodonteae						
Aegopogon bryophilus Döll	2000–3000	CHA, PRE, PUN	BEL	*Cabrera 30672* (SI)	7	A
			TUM	*Vervoorst 8499* (LIL)		
			VGR	*Burkart 11614* (BAA)		
			YAV	*Cabrera 19954* (BAA)		
Bouteloua aristidoides (Kunth) Griseb.	360–759	CHA	LED	*Cabrera 31362* (SI)	4	A
			SPE	*Cabrera 27538* (SI)		

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Bouteloua curtipendula (Michx.) Torr. var. *caespitosa* Gould & Kapadia	1080–2250	CHA, PRE	BEL	*Deginani 182* (SI)	18	P
			ECA	*Ahumada 6237* (SI)		
			SBA	*Deginani 873* (MO, SI)		
			TUM	*Deginani 340* (SI)		
Chaboissaea atacamensis (Parodi) P. M. Peterson & Annable	3343–4000	PRE, PUN	COC	*Peterson 10294* (US)	8	A
			HUM	*Deginani 478* (MO, SI)		
			RIN	*Zuloaga 6032* (SI)		
			SCA	*Okada 6707½* (SI)		
			YAV	*Peterson 10300* (US)		
Chloris barbata Sw.	578–2400	CHA, PRE	SPE	*Burkart 20147* (SI)	3	P
			TUM	*Ventura 4895* (SI)		
Chloris castilloniana Lillo & Parodi	760	CHA	ECA	*Cabrera 13672* (LP)	1	P
Chloris ciliata Sw.	578–2020	CHA, PRE	SPE	*Parodi 9796* (BAA)	2	P
			TUM	*Zuloaga 5873* (SI)		
Chloris halophila Parodi var. *humilis* Müller	1303–3000	CHA, PRE	BEL	*Cabrera 13578* (BAA)	8	P
			TIL	*Cabrera 13364* (BAA)		
			TUM	*Zuloaga 5886* (MO, SI)		
Chloris virgata Sw.	2100–2800	CHA, PRE	ECA	*Parodi 9058* (BAA)	3	A
			TUM	*Deginani 391* (SI)		
Chondrosum barbatum (Lag.) Clayton	3780–4000	ALT, PUN	RIN	*Zuloaga 6017* (SI)	4	IND
			SCA	*Morrone 2687* (SI)		
			YAV	*Zuloaga 6121* (MO, SI)		
Chondrosum simplex (Lag.) Kunth	2193–4530	ALT, PRE, PUN	COC	*Deginani 546* (SI)	26	A
			HUM	*Deginani 291* (SI)		
			RIN	*Schwabe 843* (SI)		
			SUS	*Múlgura 1251* (SI)		
			TUM	*Cabrera 34750* (SI)		
			YAV	*Deginani 681* (SI)		
Cynodon aristulatus Caro & E. A. Sánchez	600	CHA	SPE	*Sanchez 1109* (BAF)	1	P
Cynodon dactylon (L.) Pers.	460	PRE	LED	*Maldonado 788* (LP)	2	P
			TUM	*Deginani 326* (SI)		
Cynodon hirsutus Stent	3460	PRE	YAV	*Meyer 14896* (SI)	2	P
Dactyloctenium aegyptium (L.) Willd.[1]	450–1700	CHA	BEL	*Cabrera 27474* (BAA)	13	A
			ECA	*Burkart 20143* (SI)		
			LED	*Fabris 7691* (LP)		
			SBA	*Cabrera 21647* (LP)		
			SPE	*Cabrera 34675* (SI)		

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Distichlis humilis Phil.	1900–4200	ALT, PRE, PUN	HUM	*Morrone 2706* (SI)	12	P
			RIN	*Morrone 2596* (SI)		
			SUS	*Múlgura 1289* (SI)		
			TUM	*Cabrera 31734* (SI)		
			YAV	*Fries 693* (SI)		
Distichlis spicata (L.) Greene var. *andina* Beetle	2200–3420	PRE, PUN	SUS	*Castellanos 27/759* (BA)	3	P
			TUM	*Cabrera 15062* (BAA)		
			YAV	*Meyer 14930* (BAA, LIL, SI)		
Distichlis spicata (L.) Greene var. *mendocina* (Phil.) Hack.	2000–2700	PRE	TIL	*Zuloaga 3721* (MO, SI)	7	P
			TUM	*Ventura 4899* (BA, LIL, SI)		
Distichlis spicata (L.) Greene var. *stricta* (Torr.) Scribn.	2500	PRE	HUM	*Parodi 9635* (BAA, SI)	1	P
Eleusine indica (L.) Gaertn.	460–2000	CHA, YUN	BEL	*Deginani 65* (SI)	10	A
			ECA	*Ahumada 5165* (JUA)		
			LED	*Cabrera 30353* (SI)		
			SBA	*Ahumada 4880* (JUA)		
			SPE	*Ahumada 4151* (JUA, SI)		
			VGR	*Deginani 817* (SI)		
Eleusine tristachya (Lam.) Lam.	700–1300	CHA, YUN	ECA	*Ahumada 5905* (JUA)	2	A
			SBA	*Kiesling 5528* (SI)		
Eragrostis airoides Nees	1500–2000	CHA, YUN	BEL	*Zuloaga 157* (LP)	4	P
Eragrostis andicola R. E. Fr.*	1950–4000	PRE, PUN	HUM	*Zuloaga 5919* (MO, SI)	21	P
			TIL	*Cabrera 12078* (BAA, LP)		
			TUM	*Kiesling 3543* (SI)		
Eragrostis cilianensis (All.) Vignolo ex Janch.[1]	360–3500	CHA, PRE, PUN	BEL	*Burkart 11043* (SI)	25	A
			ECA	*Ahumada 5902* (JUA)		
			HUM	*Zuloaga 6042* (SI)		
			SBA	*Zuloaga 6277* (SI)		
			SPE	*Villamil 2928* (SI)		
			TIL	*Deginani 402* (SI)		
			TUM	*Deginani 393* (SI)		
Eragrostis curvula (Schrad.) Nees[1]	3500	PUN	RIN	*Zuloaga 6025* (MO, SI)	1	P
Eragrostis japonica (Thunb.) Trin.[1]	460	CHA	LED	*Vallejos 213* (LIL)	2	A
			SPE	*Villa Carenzo 1434* (LIL)		
Eragrostis lugens Nees	1300–2000	CHA, YUN	BEL	*Zuloaga 3544* (SI)	4	P
Eragrostis mexicana (Hornem.) Link	1400–2670	PRE, YUN	BEL	*Cabrera 26036* (SI)	2	A
			TIL	*Deginani 403* (SI)		

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Eragrostis montufari (Kunth) Steud.	460–3500	CHA, PRE, YUN	BEL	*Zuloaga 6145* (SI)	21	P
			ECA	*Cabrera 24641* (LP)		
			LED	*Cabrera 30981* (SI)		
			SBA	*Zuloaga 290* (LP)		
			TUM	*Morrone 2363* (MO, SI)		
			VGR	*Deginani 942* (SI)		
Eragrostis neesii Trin. var. *lindmanii* (Hack.) Ekman	1700	YUN	BEL	*Cabrera 32075* (SI)	1	P
Eragrostis nigricans (Kunth) Steud. var. *punensis* Nicora	1300–3900	CHA, PRE, PUN	BEL	*Breglia 208* (SI)	41	A
			COC	*Cabrera 9320* (BAA)		
			HUM	*Deginani 442* (SI)		
			RIN	*Claren s.n.* (CORD)		
			TUM	*Nicora 8900* (SI)		
			YAV	*Kiesling 3997* (SI)		
Eragrostis orthoclada Hack.	500–1000	CHA, YUN	ECA	*Guaglianone 1778* (SI)	5	P
			SPE	*Cabrera 27520* (SI)		
Eragrostis tenuifolia (A. Rich.) Hochst. ex Steud.[1]	600–2000	CHA, YUN	BEL	*Zuloaga 6153* (SI)	13	A
			ECA	*Cabrera 22766* (CTES, LP, SI)		
			SPE	*Cabrera 29794* (SI)		
Eragrostis trichocolea Hack. & Arechav.	2550–2600	PRE	TUM	*Deginani 351* (SI)	2	P
Eragrostis virescens J. Presl	680–2500	CHA, PRE, YUN	BEL	*Pensiero 4614* (SI)	15	A
			ECA	*Ahumada 5090* (SI)		
			LED	*Ahumada 8612* (SI)		
			SBA	*Ahumada 5990* (JUA)		
			SPE	*Ahumada 4746* (JUA)		
			TIL	*Zuloaga 6132* (MO, SI)		
			TUM	*Zuloaga 3771* (MO, SI)		
Erioneuron avenaceum (Kunth) Tateoka var. *longiglume* (Parodi) Anton	2300–3550	PRE, PUN	HUM	*Múlgura 1370* (MO, SI)	3	P
			TUM	*Ventura 4897* (SI)		
Erioneuron avenaceum (Kunth) Tateoka var. *pygmaeum* (Hack.) Anton	1400–3720	PRE, PUN	COC	*Meyer 21385* (BAA, LIL)	18	P
			HUM	*Zuloaga 5905* (MO, SI)		
			SCA	*Meyer 3151* (SI)		
			TIL	*Cristóbal 65* (LIL)		
			TUM	*Nicora 8878* (SI)		
			YAV	*Deginani 581* (SI)		
Eustachys distichophylla (Lag.) Nees	800–1700	CHA, YUN	BEL	*Cabrera 31971* (SI)	5	P
			LED	*Zuloaga 2872* (MO, SI)		

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Eustachys retusa (Lag.) Kunth	1200–1900	CHA, YUN	BEL	*Parodi 14460* (BAA)	4	P
			SAN	*Parodi 9097* (BAA)		
			SBA	*Cabrera 17274* (BAA)		
Gouinia brasiliensis (S. Moore) Swallen	800	CHA	SBA	*Costa Otero 80* (JUA)	1	P
Gouinia latifolia (Griseb.) Vasey	500–1800	CHA, YUN	BEL	*Zuloaga 5835* (SI)	12	P
			ECA	*Ahumada 6575* (JUA, SI)		
			LED	*Fabris 7302* (SI)		
			SBA	*Múlgura 1489* (SI)		
			SPE	*Cabrera 23333* (CTES)		
Leptochloa barbata (Desv.) Parodi ex Nicora	360–1700	CHA, YUN	BEL	*Deginani 13* (SI)	8	P
			LED	*Cabrera 14502* (LP)		
			SBA	*Cabrera 22304* (LP)		
			SPE	*Ahumada 4489* (SI)		
Leptochloa dubia (Kunth) Nees	1980–4500	ALT, PRE, PUN	COC	*Deginani 514* (SI)	18	P
			HUM	*Cabrera 21410* (LP)		
			TIL	*Zuloaga 6130* (SI)		
			TUM	*Zuloaga 1201* (SI)		
			YAV	*Hunziker 6035* (BAB)		
Leptochloa fusca (L.) Kunth var. *uninervia* (J. Presl) N. Snow	500–580	CHA	SBA	*Cabrera 15732* (BAA)	2	P
			SPE	*Cabrera 27531* (SI)		
Leptochloa panicea (Retz.) Ohwi var. *brachiata* (Steud.) N. Snow	360–930	CHA, YUN	ECA	*Ahumada 5162* (SI)	12	A
			LED	*Zuloaga 3654* (MO; SI)		
			SPE	*Ahumada 4145* (JUA, SI)		
Leptochloa procera Nees	460	CHA	LED	*Türpe 2753* (BAA, CTES, LIL)	1	P
Leptochloa virgata (L.) P. Beauv.	350–1700	CHA, YUN	BEL	*Kiesling 749* (LP)	23	P
			ECA	*Ahumada 5118* (JUA, SI)		
			LED	*Zuloaga 2869* (MO, SI)		
			SAN	*Parodi 9093* (BAA)		
			SBA	*Zuloaga 6300* (MO, SI)		
			SPE	*Ahumada 6119* (JUA, SI)		
Lycurus phalaroides Kunth	2340–2800	PRE	TUM	*Morrone 2381* (MO, SI)	2	P
Lycurus setosus (Nutt.) C. Reeder	2600–3720	PRE, PUN	HUM	*Morrone 2420* (MO, SI)	10	P
			TUM	*Deginani 373* (SI)		
			YAV	*Deginani 626* (SI)		
Microchloa indica (L. f.) P. Beauv.	1600	CHA	BEL	*Parodi 9808* (BAA)	2	P
Microchloa kunthii Desv.	3400	PRE	HUM	*Zuloaga 5916* (MO, SI)	1	P

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Muhlenbergia asperifolia (Nees & Meyen ex Trin.) Parodi	2100–3400	PRE, PUN	HUM	*Parodi 9669* (BAA)	10	P
			TIL	*Zuloaga 3179* (SI)		
			YAV	*Parodi 9646* (BAA)		
Muhlenbergia ciliata (Kunth) Trin.**	3700	PUN	HUM	*Venturi 8770* (MO)	1	A
Muhlenbergia fastigiata (J. Presl) Henrard**	3400–3780	PRE, PUN	COC	*Cabrera 15421* (BAA)	16	P
			HUM	*Ruthsatz s.n.* (BAA)		
			SCA	*Morrone 2693* (MO, SI)		
			YAV	*Curato 1504* (BAA)		
Muhlenbergia peruviana (P. Beauv.) Steud.	3000–4500	ALT, PRE, PUN	COC	*Múlgura 1306* (SI)	13	A
			HUM	*Múlgura 1360* (SI)		
			RIN	*s.c., s.n.* (SI 28023)		
			SCA	*Okada 6707*		
			TUM	*Cabrera 30678*		
			VGR	*Burkart 11663*		
			YAV	*Zuloaga 6065* (MO, SI)		
Muhlenbergia rigida (Kunth) Kunth	1200–4470	CHA, PRE, PUN	BEL	*Parodi 14649* (BAA)	7	P
			HUM	*Zuloaga 5961* (MO, SI)		
			SBA	*Cabrera 26216* (SI)		
			TUM	*Deginani 169* (SI)		
			YAV	*Meyer 14899* (SI)		
Muhlenbergia schreberi J. F. Gmel.	1300–2040	CHA, YUN	BEL	*Morrone 2282* (MO, SI)	14	P
			SAN	*Cabrera 34789* (SI)		
Muhlenbergia tenella (Kunth) Trin.	1400–3700	CHA, PUN, YUN	BEL	*Kiesling 70121* (SI)	5	A
			HUM	*Venturi 8770* (SI)		
			LED	*Cabrera 26457* (SI)		
			VGR	*Burkart 11579* (SI)		
Munroa andina Phil. var. *andina*	3500–4100	ALT, PRE, PUN	RIN	*Zuloaga 6021* (SI)	8	A
			SUS	*Castellanos 27/724* (BAA, SI)		
			TIL	*Cabrera 21738* (SI)		
			TUM	*Nicora 3852* (SI)		
			YAV	*Kiesling 3987* (SI)		
Munroa andina Phil. var. *breviseta* Hack.**	4100	PRE	TUM	*Nicora 8852½* (SI)	1	A
Munroa argentina Griseb.	3000–4000	PRE, PUN	HUM	*Parodi 9714* (BAA)	8	A
			TIL	*Cabrera 31597* (SI)		
			TUM	*Nicora 8783* (SI)		
			YAV	*Bolsi 167* (SI)		

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Munroa decumbens Phil.	3380–4300	ALT, PRE, PUN	HUM	*Ruthsatz s.n.* (BAA)	6	A
			RIN	*Schwabe 816* (BAA)		
			TUM	*Cabrera 31699* (SI)		
			YAV	*Bolsi 163* (SI)		
Sporobolus indicus (L.) R. Br.	1200–2950	CHA, PRE, PUN, YUN	BEL	*Morrone 2319* (SI)	18	P
			LED	*Iudica 194* (SI)		
			SBA	*Deginani 888* (SI)		
			TIL	*Venturi 4869* (BA, SI)		
			TUM	*Deginani 375* (SI)		
			VGR	*Deginani 949* (SI)		
Sporobolus phleoides Hack.	500	CHA	SPE	*Breglia 107* (JUA, SI)	1	P
Sporobolus pyramidatus (Lam.) Hitchc.	560–2670	CHA, PRE	ECA	*Zuloaga 2990* (SI)	13	P
			SBA	*Cabrera 31402* (SI)		
			SPE	*Ahumada 4144* (LIL, SI)		
			TIL	*Deginani 404* (SI)		
			TUM	*Nicora 8778* (SI)		
Sporobolus rigens (Trin.) Desv. var. *atacamensis* (Parodi) Asteg.	3500–3800	ALT, PUN	HUM	*Ruthsatz s.n.* (BAA-10658)	7	P
			SUS	*Cabrera 8737* (BAA)		
			TUM	*Cabrera 31727* (SI)		
Sporobolus rigens (Trin.) Desv. var. *rigens*	3700	PUN	COC	*Fernández 1034* (BAA)	2	P
Tragus andicola Zapater & Sulekic	2400–3400	PUN, PRE	HUM	*Soriano 691* (SI)	11	A
			TIL	*Cristóbal 62* (LIL)		
			TUM	*Nicora 8780* (SI)		
			YAV	*Zuloaga 6060* (MO, SI)		
Tragus berteronianus Schult.	740–2300	CHA, PRE	BEL	*Parodi 14463* (BAA)	3	A
			SPE	*Cabrera 31513* (SI)		
			TUM	*Venturi 4902* (LIL, SI)		
Trichloris crinita (Lag.) Parodi	2150	PRE	TUM	*Parodi 14685* (BAA)	1	P
Trichloris pluriflora E. Fourn.	460–930	CHA, PRE	BEL	*Cabrera 27502* (BAA)	4	P
			ECA	*Cabrera 14605* (BAA)		
			LED	*Parodi 14562* (BAA)		
			SPE	*Ahumada 4153* (JUA, SI)		
Tripogon spicatus (Nees) Ekman	2250–2470	PRE	TIL	*Werner 506a* (BAA)	2	P
			TUM	*Ruthsatz s.n.* (BAA)		

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Tribu Pappophoreae						
Cottea pappophoroides Kunth	580–2940	CHA, PRE	ECA	*Krapovickas 30782* (SI)	11	P
			HUM	*Burkart 11936* (SI)		
			SBA	*Múlgura 1450* (SI)		
			SPE	*Cabrera 34013* (SI)		
			TIL	*Deginani 269* (SI)		
Enneapogon desvauxii P. Beauv.	2300–3500	PRE, PUN	HUM	*Múlgura 1349* (SI)	8	P
			TIL	*Zuloaga 6124* (MO, SI)		
Pappophorum caespitosum R. E. Fr.	2070–3400	PRE, PUN	HUM	*Burkart 11949* (SI)	8	P
			TIL	*Cabrera 31608* (SI)		
			TUM	*Zuloaga 5902* (MO, SI)		
Pappophorum pappiferum (Lam.) Kuntze	360–1180	CHA	BEL	*Zuloaga 5840* (MO, SI)	3	P
			LED	*Zuloaga 3024* (MO, SI)		
Pappophorum philippianum Parodi	580	CHA	SPE	*Cabrera 27537* (SI)	1	P
Subfamilia Danthonioideae						
Tribu Danthonieae						
Cortaderia jubata (Lemoine) Stapf	2000–2150	PRE	TUM	*Kiesling 5174* (SI)	2	P
Cortaderia rudiuscula Stapf	3000–3950	PRE, PUN	COC	*Dell'Arciprete 2232* (SI)	9	P
			HUM	*Arenas 1020* (SI)		
			RIN	*Arenas 1180* (SI)		
			SCA	*Arenas 1700* (SI)		
			TIL	*Cabrera 31624* (SI)		
			TUM	*Nicora 8927* (SI)		
			YAV	*Meyer 14966* (SI)		
Cortaderia speciosa (Nees & Meyen) Stapf	2200–2900	PRE	HUM	*Hunziker 1304* (CORD)	2	P
			TUM	*Meyer 21429* (LIL)		
Lamprothyrsus hieronymi (Kuntze) Pilg.	720–3500	YUN	BEL	*Nicora 6744* (SI)	14	P
			LED	*Morrone 3534* (MO, SI)		
			SBA	*Iudica 180* (SI)		
			VGR	*Cabrera 30939* (SI)		
Subfamilia Ehrhartoideae						
Tribu Oryzeae						
Leersia hexandra Sw.	1960–2000	CHA, YUN	BEL	*Cabrera 30460* (SI)	2	P
Luziola peruviana Juss. ex J. F. Gmel.	300	YUN	BEL	*Schreiter 2953* (LIL)	1	P

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Subfamilia Panicoideae						
Tribu Andropogoneae						
Andropogon selloanus (Hack.) Hack	1500–1710	CHA, YUN	BEL	*Zuloaga 6183* (MO, SI)	2	P
Bothriochloa alta (Hitchc.) Henrard	1380–1500	CHA, YUN	BEL	*Burkart 111107* (SI)	2	P
			SBA	*Zuloaga 6367* (MO, SI)		
Bothriochloa barbinodis (Lag.) Herter	1150–2460	CHA, PRE	ECA	*Parodi 9021* (BAA)	4	P
			TIL	*Cabrera 31643* (SI)		
			TUM	*Zuloaga 6203* (MO, SI)		
Bothriochloa saccharoides (Sw.) Rydb.	3780	PUN	SCA	*Zuloaga 6113* (SI)	1	P
Elionurus muticus (Spreng.) Kuntze	1500–3300	CHA, PRE, YUN	BEL	*Zuloaga 5855* (MO, SI)	7	P
			TUM	*Parodi 14518* (BAA)		
Elionurus tripsacoides Humb. & Bonpl. ex Willd.	1980–2400	PRE, YUN	BEL	*Zuloaga 6156* (MO, SI)	6	p
			TUM	*Zuloaga 5889* (SI)		
Hemarthria altissima (Poir.) Stapf & C. E. Hubb.[1]	950	CHA	BEL	*Burkart 12014* (SI)	1	P
Heteropogon contortus (L.) P. Beauv. ex Roem. & Schult.	1620	CHA	BEL	*Parodi 14645* (BAA)	1	P
Heteropogon melanocarpus (Elliott) Benth.	460	CHA	LED	*Deginani 237* (SI)	1	A
Imperata brasiliensis Trin.	460–580	CHA	LED	*Burkart 11447* (SI)	2	P
			SPE	*Venturi 5331* (BAA)		
Imperata minutiflora Hack.	360–2000	CHA, PRE, YUN	BEL	*Burkart 11379* (SI)	9	P
			ECA	*Parodi 9095* (BAA)		
			LED	*Zuloaga 3033* (SI)		
			TUM	*Zuloaga 6339* (SI)		
Rottboellia cochinchinensis (Lour.) Clayton**[1]	460–590	CHA	LED	*Cabrera 31503* (SI)	3	A
			SPE	*Ahumada 4803* (SI)		
Schizachyrium condensatum (Kunth) Nees	1400–2000	CHA, YUN	BEL	*Zuloaga 6138* (MO, SI)	5	P
			LED	*Burkart 11416* (SI)		
Schizachyrium spicatum (Spreng.) Herter	800–2000	CHA, YUN	BEL	*Cabrera 22592* (SI)	2	P
			LED	*Zuloaga 2908* (MO, SI)		
Schizachyrium tenerum Nees	1500–3000	CHA, PRE, YUN	BEL	*Zuloaga 5860* (SI)	4	P
			HUM	*Venturi 8310* (SI)		
			HUM	*Deginani 370* (SI)		
Sorghastrum pellitum (Hack.) Parodi	1380–2100	PRE, YUN	BEL	*Hunziker 10353* (SI)	3	P
			SBA	*Zuloaga 270* (SI)		
			TUM	*Vervorst 8492* (CTES)		
Sorghastrum stipoides (Kunth) Nash	1300	CHA	BEL	*Hunziker 6131* (BAB)	1	P
Sorghum halepense (L.) Pers. var. *muticum* (Hack.) Hayek[1]	350	CHA	LED	*Costa Otero* (SI)	1	P

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Themeda quadrivalvis (L.) Kuntze[1]	1000	CHA	BEL	*Vignale 485* (SI)	1	A
Tribu Arundinelleae						
Arundinella hispida (Humb. & Bonpl. ex Willd.) Kuntze	1500	YUN	BEL	*Cabrera 30658* (SI)	1	P
Tribu Paniceae						
Anthaenantiopsis fiebrigii Parodi	1500–2100	YUN	BEL	*Zuloaga 5862* (MO, SI)	5	P
Axonopus compressus (Sw.) P. Beauv.	1400–2500	CHA, YUN	BEL	*Zuloaga 6458* (MO, SI)	13	P
			SAN	*Cabrera 34796* (SI)		
Axonopus fissifolius (Raddi) Kuhlm.	1000	CHA	BEL	*Cabrera 27310* (SI)	1	P
Axonopus siccus (Nees) Kuhlm.	1500–2800	YUN	BEL	*Zuloaga 5858* (MO, SI)	7	P
			TUM	*Deginani 377* (SI)		
Cenchrus ciliaris L.[1]	500–560	CHA	SBA	*Zuloaga 2852* (SI)	4	P
Cenchrus echinatus L.	350–800	CHA	LED	*Morrone 2754* (SI)	12	A
			SPE	*Ahumada 4472* (SI)		
Cenchrus myosuroides Kunth	560–1600	CHA	BEL	*Cabrera 30235* (SI)	8	P
			ECA	*Deginani 220* (MO, SI)		
			SBA	*Zuloaga 7090* (MO, SI)		
			SPE	*Morrone 2776* (MO, SI)		
Cenchrus pauciflorus Benth.	1200	CHA	BEL	*Krapovickas 1503* (LIL)	1	A
Digitaria aequiglumis (Hack. & Arechav.) Parodi var. *aequiglumis*	1000	YUN	BEL	*Parodi 9810* (BAA)	1	A
Digitaria aequiglumis (Hack. & Arechav.) Parodi var. *laetevirens* (Mez) Henrard	2000	CHA	BEL	*Zuloaga 3789* (SI)	1	A
Digitaria bicornis (Lam.) Roem. & Schult.	450	CHA	LED	*Zuloaga 3638* (SI)	1	A
Digitaria californica (Benth.) Henrard var. *californica*	1980–3700	PRE, PUN	TIL	*Deginani 318* (SI)	9	P
			TUM	*Zuloaga 6507* (SI)		
Digitaria californica (Benth.) Henrard var. *villosissima* Henrard	2078–3700	CHA, PRE	SPE	*Cabrera 34014* (SI)	2	P
			TUM	*Venturi 4824* (SI)		
Digitaria ciliaris (Retz.) Koeler[1]	367–2100	CHA, YUN	BEL	*Zuloaga 5836* (SI)	25	A
			ECA	*Zuloaga 3494* (SI)		
			LED	*Zuloaga 3021* (SI)		
			SBA	*Cabrera 26284* (SI)		
			SPE	*Ahumada 4205* (JUA, SI)		
			VGR	*Deginani 819a* (SI)		
Digitaria filiformis (L.) Koeler	1400–2000	CHA,YUN	BEL	*Burkart 11253* (SI)	2	A
Digitaria horizontalis Willd.	350	CHA	LED	*Costas Otero 49* (SI)	1	A

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Digitaria insularis (L.) Fedde	465–2000	CHA	BEL	*Cabrera 27506* (SI)	9	P
			LED	*Cabrera 27923* (SI)		
			SBA	*Cabrera 26269* (SI)		
			SPE	*Ahumada 4150* (JUA, SI)		
Digitaria sacchariflora (Nees) Henrard	450–1380	CHA, YUN	BEL	*Zuloaga 3619* (SI)	3	P
			LED	*Zuloaga 3022* (SI)		
			SBA	*Cabrera 26164* (SI)		
Digitaria swalleniana Henrard	1300	CHA	BEL	*Parodi 14462* (BAA)	2	P
Digitaria ternata (A. Rich.) Stapf	1180–2200	CHA, PRE, YUN	BEL	*Zuloaga 5838* (SI)	17	P
			ECA	*Cabrera 30306* (SI)		
			TUM	*Cabrera 30495* (SI)		
			VGR	*Deginani 819* (SI)		
Echinolaena minarum (Nees) Pilg.	630–2500	YUN	BEL	*Zuloaga 6162* (SI)	17	P
			LED	*Morrone 2811* (MO, SI)		
			SBA	*Morrone 3037* (MO, SI)		
			VGR	*Deginani 823* (SI)		
Echinochloa chacoensis P. W. Michael ex Renvoize	940–1800	CHA	BEL	*Zuloaga 5840* (SI)	5	A
Echinochloa colona (L.) Link	360–1700	CHA, YUN	BEL	*Parodi 14708* (BAA)	14	P
			ECA	*Zuloaga 3495* (SI)		
			LED	*Morrone 2822* (SI)		
			SBA	*Kiesling 5544* (SI)		
			SPE	*Ahumada 4818* (CTES)		
			VGR	*Deginani 825* (SI)		
Echinochloa crusgalli (L.) P. Beauv. var. *mitis* (Pursh) Peterm.	1500	CHA	BEL	*Cabrera 30217* (SI)	1	A
Echinochloa crusgalli (L.) P. Beauv. var. *zelayensis* (Kunth) Hitchc.	500–2200	CHA, PRE	ECA	*Parodi 9059* (BAA)	3	A
			SBA	*Ahumada 4887* (SI)		
			TUM	*Meyer 21412* (SI)		
Echinochloa crus-pavonis (Kunth) Schult.	360–2550	CHA, YUN	LED	*Zuloaga 2540* (SI)	5	A
			SPE	*Parodi 14567* (BAA)		
Eriochloa montevidensis Griseb.	450–1500	CHA, YUN	BEL	*Deginani 44* (SI)	6	P
			LED	*Zuloaga 3027* (MO, SI)		
			SBA	*Morrone 3044* (SI)		
			SPE	*Cabrera 27530* (SI)		
Eriochloa punctata (L.) Desv. ex Ham.	598	CHA	SPE	*Parodi 14596* (BAA)	1	P
Ichnanthus nemorosus (Sw.) Döll	465–2550	YUN	BEL	*Zuloaga 3485* (SI)	8	P
			COC	*Zuloaga 4560* (SI)		
			LED	*Zuloaga 2924* (SI)		

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Ichnanthus tarijianus K. E. Rogers	800	YUN	LED	*Zuloaga 2901* (SI)	1	P
Lasiacis sorghoidea (Desv. ex Ham.) Hitchc. & Chase	540–2600	YUN	LED	*Morrone 2882* (MO, SI)	9	P
			VGR	*Burkart 11465* (SI)		
Oplismenus hirtellus (L.) P. Beauv. subsp. *hirtellus*	1150–2100	CHA, YUN	BEL	*Deginani 10* (SI)	14	P
			ECA	*Cabrera 30330* (SI)		
			LED	*Morrone 3580* (MO, SI)		
			SBA	*Cabrera 26276* (SI)		
Oplismenus hirtellus (L.) P. Beauv. subsp. *setarius* (Lam.) Mez ex Ekman	460–1400	CHA, YUN	BEL	*Zuloaga 3006* (SI)	5	P
			LED	*Cabrera 33956* (SI)		
			SAN	*Kiesling 5500* (SI)		
			SBA			
Panicum antidotale Retz.**[1]	500	CHA	SBA	*Zuloaga 7091* (SI)	2	P
Panicum bergii Arechav.	1500	YUN	BEL	*Cabrera 32704* (SI)	1	P
Panicum capillare L.	930–1300	CHA	BEL	*Zuloaga 3060* (SI)	3	A
Panicum chloroleucum Griseb.	2600–3500	PRE, PUN	HUM	*Zuloaga 5906* (MO, SI)	6	P
			TUM	*Zuloaga 3554* (SI)		
Panicum cordovense E. Fourn.	1500–1700	YUN	BEL	*Morrone 2333* (MO, SI)	6	P
			LED	*Cabrera 26446* (SI)		
Panicum laxum Sw.	330–2500	CHA, YUN	BEL	*Deginani 153* (SI)	4	P
			LED	*Cabrera 30378* (SI)		
			SBA	*Morrone 3059* (MO, SI)		
Panicum maximum Jacq.[1]	360–1800	CHA, YUN	BEL	*Cabrera 34668* (SI)	13	P
			ECA	*Deginani 205* (SI)		
			LED	*Cabrera 34700* (SI)		
			SPE	*Cabrera 33863* (SI)		
Panicum ovuliferum Trin.	1000–2000	CHA, YUN	BEL	*Morrone 2264* (SI)	20	P
			ECA	*Cabrera 34878* (SI)		
			SBA	*Cabrera 31013* (SI)		
Panicum peladoense Henrard	1380–1500	YUN	BEL	*Zuloaga 3447* (SI)	3	P
			SBA	*Zuloaga 6368* (SI)		
Panicum sabulorum Lam. var. *polycladum* (Ekman) R. A. Palacios	580–2500	YUN	BEL	*Morrone 3219* (SI)	17	P
			LED	*Morrone 3505* (SI)		
			SPE	*Zuloaga 2060* (SI)		
			VGR	*Burkart s.n.* (SI)		
Panicum stramineum Hitchc. & Chase	350–1000	CHA	BEL	*Zuloaga 3702* (SI)	5	A
			ECA	*Ahumada 5023* (SI)		
			LED	*Costas Otero 48* (SI)		
			SPE	*Ahumada 4829* (SI)		

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Panicum trichanthum Nees	350–1700	CHA, YUN	LED	*Zuloaga 6221* (SI)	11	P
			SBA	*Cabrera 26322* (SI)		
			SPE	*Cabrera 34680* (SI)		
			VGR	*Hunziker 1973* (SI)		
Panicum trichoides Sw.	460–1300	CHA, YUN	ECA	*Zuloaga 3493* (SI)	5	A
			LED	*Morrone 3553* (SI)		
			SBA	*Zuloaga 6299* (MO, SI)		
Paspalum acuminatum Raddi	1560–2000	CHA, YUN	BEL	*Zuloaga 6191* (SI)	3	P
			ECA	*Zuloaga 5828* (SI)		
Paspalum candidum (Humb. & Bonpl. ex Flüggé) Kunth	1500–2900	YUN	BEL	*Zuloaga 6149* (SI)	12	A
			VGR	*Burkart 11618*		
Paspalum ceresia (Kuntze) Chase	1200–2800	CHA, PRE, YUN	BEL	*Morrone 2290* (MO, SI)	11	P
			HUM	*Ventura 8320*		
			SBA	*Deginani 901* (SI)		
Paspalum commune Lillo	450–2500	CHA, YUN	BEL	*Deginani 34* (SI)	28	P
			ECA	*Zuloaga 5821* (SI)		
			LED	*Cabrera 31307* (SI)		
			SBA	*Deginani 884* (SI)		
			SPE	*Krapovickas 27241* (SI)		
Paspalum conjugatum P. J. Bergius	400–1700	CHA, YUN	BEL	*Deginani 22* (SI)	14	P
			LED	*Zuloaga 6216* (SI)		
			SBA	*Morrone 2967* (SI)		
			SPE	*Ahumada 4804* (SI)		
			VGR	*Meyer 16430* (LIL)		
Paspalum denticulatum Trin.	330–1500	CHA	BEL	*Zuloaga 3679* (SI)	12	P
			SBA	*Morrone 3053* (SI)		
Paspalum dilatatum Poir.	900–1700	CHA, YUN	BEL	*Zuloaga 6192* (MO, SI)	6	P
			ECA	*Otero 59* (SI)		
Paspalum distichum L.	1200–2200	CHA, PRE, YUN	BEL	*Morrone 2266* (MO, SI)	8	P
			ECA	*Zuloaga 5823* (MO, SI)		
			LED	*Morrone 2849* (MO, SI)		
			TUM	*Meyer 21416* (LIL)		
Paspalum ekmanianum Henrard**	1500–2100	YUN	BEL	*Morrone 2330* (SI)	3	P
Paspalum humboldtianum Flüggé	1000–2500	CHA, PRE, YUN	BEL	*Morrone 2288* (MO, SI)	19	P
			ECA	*Burkart 11014* (SI)		
			SBA	*Deginani 897* (SI)		
			TUM	*Morrone 2361* (SI)		

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Paspalum inaequivalve Raddi	460	YUN	LED	*Cabrera 31331* (SI)	1	P
Paspalum malacophyllum Trin.	460–2800	CHA, PRE, YUN	BEL	*Zuloaga 3624* (SI)	29	P
			ECA	*Cabrera 30313* (SI)		
			LED	*Zuloaga 3023* (SI)		
			SBA	*Morrone 2987* (MO, SI)		
			SPE	*Parodi 9764* (BAA)		
			TUM	*Zuloaga 5898* (MO, SI)		
			VGR	*Deginani 948* (SI)		
Paspalum notatum Flüggé	460–2200	CHA, PRE, YUN	BEL	*Deginani 37* (SI)	19	P
			ECA	*Cabrera 30307*		
			LED	*Morrone 2832* (SI)		
			SAN	*Vallejas 20* (LIL)		
			SBA	*Zuloaga 2827* (SI)		
			TUM	*Cabrera 30502* (SI)		
Paspalum plicatulum Michx.	360–2200	CHA, PRE, YUN	BEL	*Morrone 2307* (MO, SI)	19	P
			ECA	*Zuloaga 5825* (MO, SI)		
			LED	*Taylor 11422*		
			TUM	*Cabrera 30498* (SI)		
Paspalum pygmaeum Hack.	1490–2950	YUN	BEL	*s. col. s.n.* (SI 16452)	3	A
			VGR	*Burkart 11670* (SI)		
Paspalum remotum J. Rémy	1100–2100	CHA, YUN	BEL	*Zuloaga 6157* (SI)	11	P
			ECA	*Zuloaga 5826* (SI)		
			LED	*Morrone 3551* (MO, SI)		
			TUM	*Castillón 383* (LIL)		
Paspalum simplex Morong	500–2000	CHA, YUN	BEL	*Cabrera 24718* (SI)	2	P
			SBA	*Ahumada 4610* (SI)		
Paspalum unispicatum (Scribn. & Merr.) Nash	820–1300	CHA	BEL	*Morrone 5839* (SI)	13	P
			ECA	*Ahumada 6234* (JUA)		
			LED	*Legname 5937* (LIL)		
			SBA	*Zuloaga 6273* (MO, SI)		
			SPE	*Morrone 2781* (MO, SI)		
Paspalum urvillei Steud.	460–1200	YUN	LED	*Morrone 2854* (SI)	2	P
Paspalum vaginatum Sw.	1300–1980	CHA, YUN	BEL	*Zuloaga 6154* (SI)	3	P
			ECA	*Zuloaga 5823* (SI)		
Paspalum virgatum L.	460	YUN	LED	*Cabrera 31307* (SI)	1	P
Paspalum volcanensis Zuloaga, Morrone & S. S. Denham**	1010–2150	PRE	TUM	*Zuloaga 5871* (SI)	2	P

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Pennisetum chilense (E. Desv.) B. D. Jacks. ex R. E. Fr.	1650–4600	ALT, PRE, PUN, YUN	COC	*Meyer 21378* (SI)	54	P
			HUM	*Morrone 2424* (MO, SI)		
			RIN	*Deginani 607* (SI)		
			SCA	*Arenas s.n.* (SI)		
			TIL	*Múlgura 1250* (SI)		
			TUM	*Deginani 342* (SI)		
			VGR	*Burkart 11896* (SI)		
			YAV	*Soriano 596* (SI)		
Pennisetum latifolium Spreng.	1300–2500	CHA, YUN	BEL	*Zuloaga 6161* (MO, SI)	14	P
			LED	*Morrone 3548* (MO, SI)		
Pennisetum montanum (Griseb.) Hack.	1980–2340	PRE	TUM	*Morrone 2405* (MO, SI)	7	P
Pennisetum nervosum (Nees) Trin.	350–460	CHA	LED	*Legname 3497* (LIL)	2	P
Pennisetum purpureum Schumach.[1]	590	CHA	SPE	*Venturi 9555* (K)	1	P
Pennisetum tristachyum (Kunth) Spreng.	460–1350	CHA, YUN	LED	*Saravia Toledo 12991* (LIL)	2	P
			VGR	*Jörgensen s.n.* (SI)		
Pseudechinolaena polystachya (Kunth) Stapf	1300–1860	YUN	BEL	*Morrone 2280* (SI)	2	IND
Rhynchelytrum repens (Willd.) C. E. Hubb.[1]	1000–2000	CHA, YUN	BEL	*Cabrera 32728* (SI)	5	P
			ECA	*Zuloaga 3822* (SI)		
Setaria adhaerans (Forssk.) Chiov.[1]	590	CHA	SPE	*Bartlett 20317* (SI)	1	A
Setaria cordobensis R. A. W. Herrm.	580	CHA	SPE	*Cabrera 27536* (SI)	1	P
Setaria glauca (L.) P. Beauv.	2070	PRE	TUM	*Schinini 22491* (SI)	1	A
Setaria hunzikeri Anton	350–1700	CHA	BEL	*Cabrera 30180* (SI)	5	P
			LED	*Cabrera 26497* (SI)		
			SPE	*Cabrera 33087* (SI)		
Setaria inopinata Toolin	730	CHA	SPE	*Parodi 14573* (SI)	1	P
Setaria lachnea (Nees) Kunth	360–2200	CHA, YUN	BEL	*Zuloaga 5847* (MO, SI)	16	P
			ECA	*Cabrera 15578* (LP)		
			SPE	*Parodi 8786* (BAA)		
			TUM	*Kurtz 11571* (CORD)		
Setaria macrostachya Kunth	730–2100	CHA, YUN	BEL	*Zuloaga 3625* (SI)	11	P
			ECA	*Cabrera 30273* (SI)		
			LED	*Fabris 5316* (BAA)		
			SBA	*Cabrera 26263* (LP)		
			SPE	*Parodi 14573* (BAA)		
Setaria magna Griseb.	460–760	CHA	ECA	*Zuloaga 407* (LP)	2	A
			SPE	*Cabrera 23424* (LP)		
Setaria mendocina Phil.	3050	PRE	HUM	*Parodi 9731* (BAA)	1	P
Setaria nicorae Pensiero	600	CHA	SBA	*Zuloaga 6759* (SI)	1	P

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Setaria oblongata (Griseb.) Parodi	460–1500	CHA, YUN	ECA	*Cabrera 19064* (LP)	9	P
			LED	*Burkart 11523* (SI)		
			SBA	*Zuloaga 6363* (MO, SI)		
			SPE	*Cabrera 27540* (SI)		
Setaria pampeana Parodi ex Nicora	2150	PRE	TUM	*Parodi 14686* (BAA)	1	P
Setaria parviflora (Poir.) Kerguélen	460–2550	CHA, YUN	BEL	*Nicora 8717* (SI)	13	P
			LED	*Cabrera 30366* (SI)		
			SBA	*Kiesling 5368* (SI)		
			TUM	*Cabrera 15563* (LP)		
			VGR	*Deginani 815* (SI)		
Setaria pflanzii Pensiero	600	CHA	SBA	*Zuloaga 6261* (MO, SI)	1	P
Setaria scandens Schrad.	1500–1700	YUN	BEL	*Cabrera 23722* (LP)	2	A
			ECA	*Cabrera 30332* (SI)		
Setaria vulpiseta (Lam.) Roem. & Schult.	350–650	YUN	LED	*Zuloaga 6313* (SI)	2	P
Steinchisma hians (Elliott) Nash	1100–2000	CHA, YUN	BEL	*Zuloaga 3012* (SI)	9	P
Urochloa adspersa (Trin.) R. D. Webster	460–1300	CHA	BEL	*Cabrera 27477* (SI)	28	A
			ECA	*Cabrera 26479* (SI)		
			LED	*Zuloaga 3634* (SI)		
			SBA	*Morrone 3033* (MO, SI)		
			SPE	*Ahumada 4464* (SI)		
Urochloa fusca (Sw.) B. F. Hansen & Wunderlin	460–600	CHA	LED	*Morrone 2914* (MO, SI)	7	A
			SBA	*Cabrera 31414* (SI)		
Urochloa lorentziana (Mez) Morrone & Zuloaga	500–1960	CHA, YUN	BEL	*Cabrera 30606* (SI)	14	A
			ECA	*Zuloaga 3496* (SI)		
			SBA	*Ahumada 4873* (SI)		
			SPE	*Cabrera 30236* (SI)		
Urochloa mutica (Forssk.) T. Q. Nguyen[1]	460–600	CHA	LED	*Cabrera 31504* (SI)	4	P
			SPE	*Reales 1467* (SI)		
Urochloa panicoides P. Beauv.[1]	300–1500	CHA, YUN	BEL	*Zuloaga 2996* (SI)	24	A
			ECA	*Ahumada 5166* (SI)		
			LED	*Zuloaga 2518* (MO, SI)		
			SBA	*Morrone 2994* (MO, SI)		
			SPE	*Cabrera 34683* (SI)		
Urochloa paucispicata (Morong) Morrone & Zuloaga	330–680	CHA	LED	*Zuloaga 3019* (SI)	6	A
			SPE	*Morrone 3589* (MO, SI)		

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Urochloa plantaginea (Link) R. D. Webster[1]	360–2500	CHA, YUN	BEL	*Zuloaga 3005* (SI)	21	P
			ECA	*Zuloaga 3014* (SI)		
			LED	*Zuloaga 3018* (SI)		
			SBA	*Cabrera 20152* (SI)		
			SPE	*Cabrera 30262* (SI)		
			VGR	*Deginani 847* (SI)		
Urochloa platyphylla (Munro ex C. Wright) R. D. Webster	590–1960	CHA	BEL	*Zuloaga 3668* (SI)	7	A
			ECA	*Zuloaga 2991* (SI)		
			SPE	*Bartlett 20299* (LP)		
Subfamilia Pharoideae						
Tribu Phareae						
Pharus lappulaceus Aubl.	460–1140	YUN	LED	*Zuloaga 6246* (MO, SI)	8	P
			SBA	*Cabrera 34877* (SI)		
Subfamilia Pooideae						
Tribu Bromeae						
Bromus auleticus Trin. ex Nees	2040	PRE	TUM	*Morrone 3171* (MO, SI)	1	P
Bromus berteroanus Colla	3200	PRE	TUM	*Cabrera 15141* (SI)	1	A
Bromus brachyanthera Döll	1700–2130	YUN	BEL	*Parodi 14523* (BAA)	2	P
Bromus catharticus Vahl	1700–4300	PRE, PUN, YUN	BEL	*Zuloaga 3391* (SI)	35	IND
			COC	*Deginani 504* (SI)		
			HUM	*Deginani 431*(SI)		
			LED	*Türpe 2785* (LIL)		
			RIN	*Deginani 563* (SI)		
			SCA	*Kurtz 11415* (CORD)		
			TIL	*Meyer 14946* (SI)		
			TUM	*Zuloaga 3581* (SI)		
			VGR	*Burkart 11757* (SI)		
			YAV	*Meyer 11971* (LIL)		
Bromus flexuosus Planchuelo	1400–4500	ALT, PUN, YUN	BEL	*Cabrera 15491* (BAA)	6	P
			RIN	*Schinini 773* (BAA)		
			VGR	*Burkart 11552* (SI)		
			YAV	*Cabrera 15307* (BAA)		
Bromus lanatus Kunth	3500–5000	PUN	HUM	*Cabrera 27430* (SI)	6	P
			VGR	*Burkart 11920* (BAA, SI)		
			YAV	*Deginani 690* (SI)		

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Bromus madritensis L.[1]	1000	CHA	ECA	*Cabrera s.n.* (BAB)	1	A
Bromus villosissimus Hitchc.	4500	PUN	HUM	*Morrone 2475* (MO, SI)	1	P
Tribu Meliceae						
Melica adhaerens Hack.	3700–3900	PRE, PUN	HUM	*Cabrera 15500* (LP)	3	P
			TIL	*Cabrera 12099* (SI)		
Melica chilensis J. Presl	2300–2900	PRE	TUM	*Castillón 665b* (LIL)	2	P
Melica sarmentosa Nees var. *monticola* Torres	1350–1500	YUN	BEL	*Rial Alberti s.n.* (BAB)	3	P
			SBA	*de la Sota 2950* (LP)		
			VGR	*Fabris 3586* (LP)		
Tribu Poeae						
Agrostis inconspicua Kunze ex E. Desv.	2000	YUN	SBA	*Legname 5138* (LP)	1	P
Agrostis kuntzei Mez	3450	PUN	YAV	*Meyer 14912* (SI)	1	P
Agrostis montevidensis Spreng. ex Nees fo. *montevidensis*	1200–2500	CHA, YUN	BEL	*Cabrera 21581* (BAA)	11	P
			SBA	*Guaglianone 1856* (SI)		
			TUM	*Castillón 9374* (LIL)		
Agrostis montevidensis Spreng. ex Nees fo. *submutica* (Döll) Kämpf	2000–2040	YUN	BEL	*Zuloaga 6148* (MO, SI)	2	P
Agrostis perennans (Walter) Tuck.	2200–3000	PRE, YUN	TUM	*Cabrera 16931* (LP)	3	P
			VGR	*Burkart 11653* (SI)		
Agrostis tolucensis Kunth	4300	PUN	SCA	*Claren s.n.* (SI)	2	P
Alopecurus hitchcockii Parodi**	3780	PUN	RIN	*Deginani 565* (SI)	1	A
Anthochloa lepidula Nees & Meyen	4000–5170	PUN	HUM	*Cabrera 20719* (LP)	4	P
			RIN	*Schwabe 1025* (LP)		
Avena fatua var. *pilosissima*[1]	2461–3600	PRE, PUN	HUM	*Parodi 9740* (BAA)	3	A
			SCA	*Arenas s.n.* (SI)		
			TIL	*Ambrosetti s.n.* (SI)		
Briza monandra (Hack.) Pilg.	465–2900	PRE, YUN	BEL	*Zuloaga 3539* (SI)	6	P
			LED	*Ramadori 174* (SI)		
			TUM	*Kiesling 5795* (SI)		
			VGR	*Deginani 922* (SI)		
Briza subaristata Lam.	1000	CHA	BEL	*Castillon 2668* (LIL)	1	P
Briza uniolae (Nees) Nees ex Steud.	1500–2100	YUN	BEL	*Zuloaga 3466* (SI)	5	P
Catabrosa werdermannii (Pilg.) Nicora & Rúgolo	3600–4530	ALT, PUN	RIN	*Morrone 2548* (MO, SI)	2	P
			SUS	*Breglia 244* (JUA)		
Chaetotropis elongata (Kunth) Björkman	720–2000	CHA, YUN	BEL	*Zuloaga 3424* (SI)	10	P
			LED	*Kiesling 8210* (SI)		
			VGR	*Cabrera 27884* (SI)		

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Chaetotropis hackelii (R. E. Fr.) Björkman	3300–3780	PUN	COC	*Cabezas 14* (SI)	5	P
			RIN	*Deginani 568* (SI)		
			YAV	*Meyer 14957* (LIL)		
Chaetotropis imberbis (Phil.) Björkman	2080–3050	PRE	HUM	*Parodi 9745* (BAA)	2	P
			TUM	*Nicora 8775* (SI)		
Deyeuxia breviaristata Wedd.	3690–4650	ALT, PRE, PUN	COC	*Deginani 549* (SI)	8	P
			HUM	*Morrone 2440* (MO, SI)		
			RIN	*Morrone 2571* (SI)		
Deyeuxia brevifolia J. Presl	3300–4300	ALT, PRE, PUN	HUM	*Meyer 21364* (LIL)	3	P
			RIN	*Zuloaga 6024* (MO, SI)		
Deyeuxia cabrerae (Parodi) Parodi var. *aristulata*** Rúgolo & X. Villavicencio	4300–4370	PUN	HUM	*Ruthsatz 444/4* (SI)	2	P
Deyeuxia cabrerae (Parodi) Parodi var. *cabrerae*	4000	PUN	SUS	*Cabrera 8290* (BAA)	1	P
Deyeuxia cabrerae (Parodi) Parodi var. *maxima** Rúgolo	3500	PUN	COC	*Cabrera 15404* (BAA)	1	P
Deyeuxia calderillensis (Pilg.) Rúgolo	4500	PUN	TIL	*Budin 1512* (BAA)	1	P
Deyeuxia chrysantha J. Presl var. *chrysantha***	3950	PUN	RIN	*Schwabe 1015* (BAA)	1	P
Deyeuxia chrysantha J. Presl var. *phalaroides* (Wedd.) X. Villavicencio	4530	ALT	RIN	*Morrone 2552* (SI)	1	P
Deyeuxia chrysophylla Phil.	4100–4300	ALT, PUN	RIN	*Schwabe 739* (BAA)	2	P
			TUM	*Valla 18429* (BAA)		
Deyeuxia colorata Beetle	1380–3500	CHA	SBA	*Zuloaga 6370* (SI)	2	P
			VGR	*Boelcke 11743* (BAA)		
Deyeuxia crispa Rúgolo & X. Villavicencio	3950–4900	ALT, PUN	HUM	*Cabrera 20772* (BAA)	4	P
			RIN	*Arenas s.n.* (SI)		
			SUS	*Werner 151* (BAA)		
Deyeuxia curvula Wedd.	3750–4530	ALT, PUN	COC	*Morrone 2531* (MO, SI)	4	P
			RIN	*Morrone 2560* (SI)		
Deyeuxia deserticota Phil. var. *breviaristata* Rúgolo & X. Villavicencio	4950	PUN	HUM	*Ruthsatz 1/4* (SI)	1	P
Deyeuxia deserticola Phil. var. *deserticola*	4700–4850	PUN	HUM	*Fernández 1006* (BAA)	3	P
Deyeuxia eminens J. Presl var. *eminens*	3450–4500	ALT, PUN	HUM	*Zuloaga 5951* (SI)	6	P
			RIN	*Morrone 2536* (SI)		
			SUS	*Cabrera 317444* (SI)		
			YAV	*Deginani 579* (SI)		
Deyeuxia eminens J. Presl var. *fulva* (Griseb.) Rúgolo	3500	PUN	COC	*Venturi 10214* (US)	1	P
Deyeuxia fiebrigii (Pilg.) Rúgolo	4500–4530	PUN	HUM	*Morrone 2479* (SI)	2	P
			YAV	*Zuloaga 6089* (MO, SI)		
Deyeuxia filifolia Wedd.	2200–3600	PRE, PUN	TUM	*Schreiter 2965* (LIL)	2	P
			YAV	*Cabrera 15368* (BAA)		

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Deyeuxia hackelii (Lillo) Parodi	4000–4300	ALT, PUN	HUM	*Petersen 99* (BAA)	3	P
			RIN	*Schwabe 1058* (BAA)		
			SUS	*Cabrera 8280* (BAA)		
Deyeuxia heterophylla Wedd.	3690–4300	ALT, PUN	HUM	*Fernández s.n.* (BAA)	4	P
			TUM	*Cabrera 30581* (SI)		
			RIN	*Zuloaga 6029* (SI)		
Deyeuxia hieronymi (Hack.) Türpe	2100–4500	PRE, PUN, YUN	HUM	*Budin 7479* (BAA)	3	P
			SBA	*Cabrera 17312* (BAA)		
			TIL	*Budin 1512* (BAA)		
Deyeuxia lagurus Wedd.	4700	ALT	HUM	*Hunziker 6120* (BAA)	1	P
Deyeuxia malamalensis (Hack.) Parodi	2600–4600	PRE, PUN, YUN	TIL	*Cabrera 14059* (BAA)	4	P
			VGR	*Deginani 921* (SI)		
Deyeuxia nardifolia (Griseb.) Phil.	4530	PUN	YAV	*Zuloaga 6093* (SI)	1	P
Deyeuxia orbignyana Wedd.**	3400–4100	PUN	COC	*Claren s.n.* (CORD)	3	P
			HUM	*Hunziker 10563* (SI)		
			YAV	*Hitchcock 22902* (US)		
Deyeuxia polygama (Griseb.) Parodi	1710–2000	YUN	BEL	*Zuloaga 6187* (SI)	3	P
			VGR	*Fabris 5885* (BAA)		
Deyeuxia recta Kunth**	4000	PUN	HUM	*Zuloaga 5983* (SI)	1	P
Deyeuxia rigescens (J. Presl) Türpe	3420–3870	PUN	HUM	*Deginani 435* (SI)	3	P
			SCA	*Morrone 2695* (SI)		
			YAV	*Zuloaga 6061* (SI)		
Deyeuxia rigida Kunth	4440	PUN	YAV	*Zuloaga 6080* (MO, SI)	1	P
Deyeuxia sclerantha (Hack.) Rúgolo & Villav.	3000	PUN	VGR	*Burkart 11785a* (SI)	1	P
Deyeuxia setiflora Wedd.**	3890	PUN	TUM	*Nicora 8806* (SI)	1	P
Deyeuxia spicigera J. Presl	3600–3690	PUN	SCA	*Deginani 576* (SI)	2	P
			YAV	*Meyer s.n.* (BAA-14935)		
Deyeuxia tarmensis (Pilg.) Sodiro var. *tarijensis* (Pilg.) X. Villavicencio	3500–4500	PUN	HUM	*Arenas s.n.* (SI)	3	P
			SCA	*Zuloaga 6109* (SI)		
Deyeuxia trichodonta Wedd.	2200–3800	PRE, PUN	TUM	*Cabrera 26358* (SI)	3	P
			VGR	*Fabris 5428* (BAA)		
Deyeuxia vicunarum Wedd.	4110	PUN	HUM	*Zuloaga 5947* (SI)	1	P
Deyeuxia violacea Wedd. var. *puberula* Rúgolo & X. Villavicencio	3200	PUN	VGR	*Burkart 11760* (SI)	1	P
Deyeuxia violacea Wedd. var. *violacea*	4000	PUN	VGR	*Burkart 11876* (SI)	1	P
Deyeuxia viridiflavescens (Poir.) Kunth var. *montevidensis* (Nees) Cabrera & Rúgolo	2000	PRE	TUM	*Parodi 14627* (BAA)	1	P

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Deyeuxia viridiflavescens (Poir.) Kunth var. *viridiflavescens*	1500	YUN	BEL	*Cabrera 31932* (SI)	1	P
Dielsiochloa floribunda (Pilg.) Pilg.	4750–5010	PRE, PUN	HUM	*Ruthsatz 493/1* (BAA)	4	P
Dissanthelium peruvianum (Nees & Meyen) Pilg.**	4100	PUN	BEL	*Tovar 6246* (USM)	1	A
Festuca acanthophylla E. Desv.	3200	PRE	TUM	*Cabrera 18366* (LP)	1	P
Festuca argentinensis (St.-Yves) Türpe	2900–4900	PRE, PUN	HUM	*Fernández 1002* (BAA)	4	P
			TIL	*Krapovickas 17607* (LP)		
			TUM	*Cabrera 22507* (LP)		
Festuca buchtienii Hack.	1500–4300	ALT, PRE, PUN	COC	*Cabrera 9287* (BAA)	4	P
			RIN	*Breglia 142* (SI)		
			TUM	*Taylor 11217* (SI)		
Festuca chrysophylla Phil.	3700–4200	ALT, PRE, PUN	RIN	*Cabrera 9342* (BAA, BAB)	3	P
			TUM	*Nicora 8345* (SI)		
Festuca deserticola Phil.	3400–4200	PUN	COC	*Fabris 7780* (LP)	2	P
			SUS	*Cabrera 8281* (LP)		
Festuca dissitiflora Steud. ex Griseb.	2600–4000	PRE, PUN	BEL	*Fabris 4108* (BAA, LP)	4	P
			TUM	*Kiesling 5199* (SI)		
			SUS	*Stipanicich 15221* (BAA, SI)		
Festuca distichovaginata Pilg.	4700	PUN	HUM	*Hunziker 10604* (SI)	1	P
Festuca eriostoma Hack.	3600–4400	PRE, PUN	HUM	*Fernández 1030* (BAA)	9	P
			RIN	*Cabrera 9327* (BAA)		
			SCA	*Arenas 1790* (SI)		
			SUS	*Cabrera 8620* (LP)		
			TUM	*Cabrera 30528* (SI)		
			VGR	*Burkart 11825* (SI)		
Festuca fiebrigii Pilg.	2800–4530	PRE, PUN, YUN	HUM	*Hunziker 10546* (SI)	6	P
			LED	*Fabris 5897* (LP, SI)		
			TIL	*Cabrera 14060* (BAA, LP)		
			VGR	*Burkart 11710* (BAA, SI)		
			YAV	*Deginani 679* (SI)		
Festuca hieronymi Hack.	1300–4200	PRE, PUN, YUN	BEL	*Zuloaga 6142* (SI)	27	P
			COC	*Cabrera 15266* (BAB)		
			HUM	*Cabrera 18994* (LP)		
			SAN	*Picchetti 12* (SI)		
			TIL	*Cabrera 13293* (LP)		
			TUM	*Zuloaga 5891* (SI)		
			VGR	*Deginani 919* (SI)		
			YAV	*Cabrera 15367* (LP)		

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Festuca humilior Nees & Meyen	3090–4440	ALT, PUN	COC	*Cabrera 15271* (BAA, LP)	7	P
			HUM	*Zuloaga 5984* (SI)		
			RIN	*Cabrera 7775* (LP)		
			SCA	*Deginani 572* (SI)		
			YAV	*Zuloaga 6084* (MO, SI)		
Festuca hypsophila Phil.**	4300–4600	ALT, PUN	HUM	*Morrone 2502* (SI)	3	P
			RIN	*Schwabe 211* (BAA, LIL)		
			SUS	*Cabrera 22520* (LP)		
Festuca lasiorrhachis Pilg.	3600–4450	PUN	COC	*Cabrera 9308* (LP)	4	P
			HUM	*Breglia 65* (SI)		
			TUM	*Cabrera 31676* (SI)		
			YAV	*Yavi 7778* (LP, SI)		
Festuca lilloi Hack.	2000–3400	PRE, YUN	BEL	*Burkart 11308* (SI)	2	P
			TIL	*Cabrera 14049* (BAA)		
Festuca nardifolia Griseb. var. *calchaquiensis* (Hack.) St.-Yves	4100–4700	ALT, PUN	HUM	*Cabrera 9210* (LP)	3	P
Festuca nardifolia Griseb. var. *nardifolia*	4600	PUN	VGR	*Burkart 11847* (LIL, SI)	1	P
Festuca nemoralis Türpe	4100–4700	PRE, YUN	BEL	*Cabrera 31547* (SI)	15	P
			LED	*Iudica 217* (SI)		
			SBA	*Fabris 5109* (LP)		
			TIL	*Fabris 6503* (LP)		
			VGR	*Fabris 5796* (LP)		
Festuca orthophylla Pilg.	3500–4800	ALT, PUN	COC	*Cabrera 9425* (BAB)	20	P
			HUM	*Venturi 8734* (SI)		
			RIN	*Deginani 611* (SI)		
			SCA	*Cabrera 17662* (LP)		
			TUM	*Kiesling 5307* (SI)		
			VGR	*Burkart 11823* (SI)		
			YAV	*Cabrera 21514* (LP)		
Festuca parodiana (St.-Yves) Nicora	2000–2900	PRE, YUN	BEL	*Zuloaga 6147* (SI)	5	P
			TIL	*Krapovickas 17645* (LP)		
Festuca subulata Trin.	1600	YUN	BEL	*Deginani 199* (SI)	1	P
Festuca superba Parodi ex Türpe*	1445–2500	YUN	BEL	*Nicora 8740* (SI)	13	P
Festuca ulochaeta Nees ex Steud.	1600–1980	YUN	BEL	*Zuloaga 3434* (SI)	2	P
			SBA	*Türpe 2746* (LIL)		
Festuca uninodis Hack.	3400	PUN	COC	*Vignati 439* (LP)	1	P

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Festuca villipalea (St.-Yves) E. B. Alexeev	3500–4500	PUN	HUM	*Zuloaga 5924* (MO, SI)	3	P
			RIN	*de la Sota 4220* (SI)		
			VGR	*Burkart 11835* (SI)		
Festuca weberbaueri Pilg.	3700–3850	PUN	HUM	*Soriano 649* (LIL, SI)	3	P
			TUM	*Sleumer 3229* (LIL, SI)		
			VGR	*Burkart 11810* (SI)		
Koeleria kurtzii Hack. ex Kurtz	3000–4500	PUN, YUN	BEL	*Burkart 11282* (BAA)	5	A
			HUM	*Morrone 2500* (MO, SI)		
			VGR	*Burkart 11785* (BAA)		
Lolium multiflorum Lam.[1]	3000–3440	PUN	COC	*Parodi 15151* (BAA)	3	A
			TUM	*Zuloaga 3578* (SI)		
			YAV	*Meyer 21273* (BAA)		
Lolium perenne L.[1]	4500	PUN	HUM	*Schwabe 523* (BAB)	1	P
Phalaris angusta Nees ex Trin.	1300–2060	CHA, YUN	BEL	*Cabrera 34547* (SI)	7	A
			SPE	*Eyerdam 22556* (SI)		
Poa anfamensis Negritto & Antón	3570	PUN	YAV	*Deginani 583* (SI)	1	A
Poa annua L.[1]	1400–4140	PRE, PUN, YUN	BEL	*Kiesling 1123* (SI)	12	A
			COC	*Cabezas 11* (SI)		
			HUM	*Deginani 437* (SI)		
			LED	*Cabrera 26428* (SI)		
			RIN	*Kurtz 11614* (BAA, CORD, SI)		
			SCA	*Kurtz 11407* (CORD)		
			TIL	*Kiesling 374* (LP)		
			TUM	*Morrone 2728* (SI)		
			YAV	*Meyer 14904* (LIL, SI)		
Poa calchaquiensis Hack.	1200–4600	PRE, PUN, YUN	BEL	*Morrone 3278* (SI)	26	P
			COC	*Deginani 538* (SI)		
			HUM	*Morrone 2522* (MO, SI)		
			RIN	*Kurtz 11611* (CORD)		
			SBA	*Cabrera 22236* (BAA)		
			SCA	*Cabrera 17691* (LP)		
			SUS	*Werner 76* (LP)		
			TIL	*Werner 596* (LP)		
			TUM	*Nicora 8894* (CORD, SI)		
			VGR	*Fabris 3627* (LP)		
			YAV	*Cabrera 15297* (BAA)		

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Poa chamaeclinos Pilg.	4100–4600	PUN, YUN	TIL	*Cabrera 14066* (BAA)	2	P
			VGR	*Burkart 11908* (SI)		
Poa dolichophylla Hack.	2000	YUN		*Fabris 2875* (LP)	1	P
Poa grisebachii R. E. Fr.*	3650	PUN	SCA	*Kurtz 11412* (BAA)	1	P
Poa gymnantha Pilg.	4000	PUN	YAV	*Cabrera 7828* (LP)	1	P
Poa hieronymii Hack.	1700–2000	YUN	BEL	*Zuloaga 5857* (SI)	1	P
			LED	*Legname 7948* (W)		
Poa kurtzii R. E. Fr.	3400–4700	PRE, PUN	BEL	*Fabris 4014* (LP)	14	P
			HUM	*Morrone 2581* (MO, SI)		
			RIN	*Kurtz 11598* (BAA, CORD)		
			SCA	*Kurtz 11584* (BAA, CORD)		
			TIL	*Cabrera 14060* (BAA)		
			VGR	*Burkart 11903* (BAA, SI)		
			YAV	*Deginani 686* (SI)		
Poa laetevirens R. E. Fr.	3500–3800	PUN	RIN	*Kurtz 11614a* (BAA, BAF, CORD)	2	P
			TUM	*Fries 806* (BAA)		
Poa lilloi Hack.	3890–4850	PRE, PUN	HUM	*Morrone 2490* (MO, SI)	7	P
			RIN	*Morrone 2541* (SI)		
			TUM	*Nicora 8810* (SI)		
Poa myriantha Hack.	1400–1700	YUN	LED	*Cabrera 26430* (SI)	3	P
			VGR	*Burkart 11580* (BAA, CORD, SI)		
Poa parviceps Hack. var. *jujuyensis* Parodi ex Nicora	4600–4700	PUN	HUM	*Meyer 21217* (BAA)	3	P
			VGR	*Burkart 11893a* (SI)		
Poa parviceps Hack. var. *parviceps*	4000–4300	ALT, PUN	RIN	*Schwabe 908* (CORD, SI)	3	P
			VGR	*Burkart 11893* (SI)		
			YAV	*Cabrera 7838* (BAA)		
Poa perligulata Pilg.	3000–4650	ALT, PUN	HUM	*Cabrera 9208* (BAA)	4	P
			RIN	*Schwabe 4600* (LP)		
			VGR	*Burkart 11881* (SI)		
Poa pratensis L.	3700	PUN	YAV	*Novara 8258* (MCNS)	1	P
Poa scaberula Hook. f.	3600	PUN	SCA	*Kurtz 11483* (CORD)	1	A
Poa superata Hack.	2800–3480	PRE, PUN	BEL	*Fabris 4124* (LP)	5	P
			HUM	*Kiesling 650* (LP)		
			TIL	*Cabrera 13277* (LP)		
			TUM	*Lillo 44043* (LP)		

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Poa trivialis L.	4000	PUN	HUM	*Fernández s.n.* (BAA)	1	P
Polypogon interruptus Kunth	2070–3900	PRE, PUN	COC	*Cabezas 15* (SI)	21	P
			HUM	*Meyer 21090* (LIL)		
			SCA	*Zuloaga 6105* (SI)		
			TIL	*Kiesling 351* (LP)		
			TUM	*Morrone 2742* (SI)		
			VGR	*Kiesling 456* (LP)		
			YAV	*Meyer 14961* (SI)		
Polypogon monspeliensis (L.) Desf.[1]	460–3500	PRE, PUN, YUN	BEL	*Schreiter 2949* (LIL)	10	A
			HUM	*Claren 11720* (SI)		
			LED	*Venturi 10648* (SI)		
			TIL	*Fabris 6334* (BAA, LP)		
			TUM	*Cabrera 34621* (SI)		
			YAV	*Meyer 14903* (SI)		
Polypogon viridis (Gouan) Breistr.[1]	960–3900	PRE, PUN, YUN	LED	*Zuloaga 6223* (MO, SI)	11	P
			TUM	*Morrone 2740* (SI)		
			VGR	*Ahumada 8731* (SI)		
Puccinellia argentinensis (Hack.) Parodi	2200–4100	PRE, PUN	TIL	*Claren s.n.* (BAA)	5	P
			TUM	*Nicora 8867* (SI)		
			YAV	*Hauman s.n.* (BA, BAA, SI)		
Puccinellia frigida (Phil.) I. M. Johnst.	3660–4600	ALT, PUN	COC	*Deginani 554* (SI)	12	P
			HUM	*Venturi 8720* (BAA, LIL)		
			RIN	*Morrone 2570* (MO, SI)		
			SCA	*Deginani 573* (SI)		
			SUS	*Cabrera 8961* (BAA)		
			VGR	*Ruthsatz s.n.* (BAA)		
			YAV	*Parodi 9626* (BAA)		
Vulpia bromoides (L.) Gray[1]	1500	YUN	BEL	*Schinini 10101* (BAA)	1	A
Vulpia myuros (L.) C. C. Gmel.[1]	1980–3780	PRE, PUN, YUN	BEL	*Zuloaga 3413* (SI)	10	A
			HUM	*Vallejos 141* (LIL)		
			SCA	*Zuloaga 6107* (MO, SI)		
			TUM	*Zuloaga 6202* (MO, SI)		
			VGR	*Burkart 11713* (SI)		
Tribu Stipeae						
Anatherostipa bomanii (Hauman) Peñailillo**	3700–4400	ALT, PUN	RIN	*Schwabe 1143* (BAA)	5	P
			SUS	*Cabrera 8403* (LP)		

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Anatherostipa brevis (Torres) Peñailillo*	3000–3400	PRE, PUN	TIL	*Cabrera 14047* (BAA)	3	P
			TUM	*Cabrera 18311* (LP)		
			VGR	*Burkart 11801* (SI)		
Anatherostipa henrardiana (Parodi) Peñailillo*	4900–4600	ALT, PUN	RIN	*Schwabe 1069* (LP)	2	P
			SUS	*Cabrera 9105* (BAA)		
Anatherostipa mucronata (Griseb.) F. Rojas	2500–4700	ALT, PRE, PUN	HUM	*Fernández 1021* (LIL)	7	P
			RIN	*Schwabe 705* (LP)		
			TIL	*Werner 584b* (BAA)		
			TUM	*Cabrera 22477* (LP)		
Jarava frigida (Phil.) F. Rojas	3920	PUN	SUS	*Hueck 487* (BA)	1	P
Jarava leptostachya (Griseb.) F. Rojas	2200–4600	ALT	BEL	*Fabris 4047* (LP)	15	P
		PRE, PUN	COC	*Venturi 9362* (SI)		
			HUM	*Zuloaga 5982* (SI)		
			RIN	*Schwabe 953* (LP)		
			SCA	*Okada 3913* (LP)		
			SUS	*Cabrera 8751* (LP)		
			TIL	*Budin 2232* (SI)		
			TUM	*Cabrera 26360* (LP)		
			YAV	*Cabrera 15321* (LP)		
Jarava plumosa (Spreng.) S. W. L. Jacobs & J. Everett	2200–3600	PRE, PUN	SCA	*Claren s.n.* (CORD)	2	P
			TUM	*Castillo 2046* (LIL)		
Jarava pseudoichu (Caro) F. Rojas	1380–2600	PRE, YUN	BEL	*Zuloaga 132* (SI)	5	P
			SBA	*Cabrera 17342* (LP)		
			TIL	*Cabrera 13227* (LP)		
Jarava pungens (Nees & Meyen) Matthei	3000–4300	ALT, PRE, PUN	BEL	*Fabris 4112* (LP)	7	P
			HUM	*Cabrera 21420* (LP)		
			RIN	*Zuloaga 6010* (MO, SI)		
			TUM	*Cabrera 15156* (LP)		
			YAV	*Meyer 114900* (LIL)		
Jarava vaginata (Phil.) F. Rojas	2500–3800	PRE, PUN	COC	*Cabrera 15406* (LP)	5	P
			HUM	*Burkart 11959* (SI)		
			TIL	*Cabrera 13330* (LP)		
			TUM	*Cabrera 22434* (LP)		
			YAV	*Cabrera 15335* (LP)		
Vassella arcaensis (Speg.) Torres	2200–3300	PRE, PUN	HUM	*Meyer 21073* (LIL)	3	P
			TUM	*Cabrera 16866* (SI)		

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Nassella arcuata (R. E. Fr.) Torres	2600–3900	PUN	COC	*Deginani 493* (SI)	15	P
			HUM	*Zuloaga 5969* (MO, SI)		
			SCA	*Cabrera 17667* (LP)		
			TIL	*Cabrera 12133* (LP)		
			TUM	*Cabrera 263731/2* (LP)		
			YAV	*Meyer s.n.* (LIL)		
Nassella cabrerae Torres	3440–3690	PUN	COC	*Cabrera 9299* (LP)	4	P
			RIN	*Zuloaga 6031* (SI)		
			YAV	*Parodi 9655* (BAA)		
Nassella caespitosa Griseb.	3350–4000	PRE, PUN	HUM	*Claren 11701*(SI)	4	P
			SCA	*Deginani 647* (SI)		
			TUM	*Cabrera 15157* (LP)		
Nassella clarazii (Ball) Barkworth	1200–2800	CHA, PRE	SBA	*Cabrera 26260* (LP)	3	P
			TUM	*Deginani 368* (SI)		
Nassella curviseta (Hitchc.) Barkworth	1850–4000	PRE, PUN	COC	*Cabrera 15274* (LP)	8	P
			HUM	*Fabris 7431* (LP)		
			SCA	*Deginani 649* (SI)		
			TUM	*Kiesling 3521* (SI)		
			YAV	*Cabrera 15296a* (SI)		
Nassella dasycarpa (Hitchc.) Torres	3500	PUN	HUM	*Fernández s.n.* (BAA)	1	P
Nassella depauperata (Pilg.) Barkworth var. *depauperata*	4300–4600	ALT, PUN	HUM	*Zuloaga 5980* (MO, SI)	4	P
			RIN	*Schwabe 1016* (LP)		
			YAV	*de la Sota 4099* (LP)		
Nassella depauperata (Pilg.) Barkworth var. *glabrata* (Pilg.) Torres	4000	PUN	TIL	*Cabrera 12132* (LP)	1	P
Nassella elata (Speg.) Torres	2900–2200	PRE, PUN	HUM	*Marchessi s.n.* (BAA)	2	P
			TUM	*Cabrera 16281* (LP)		
Nassella glabripoda Torres var. *glabripoda*	3500–4450	PUN	HUM	*Ruthsatz s.n.* (BAA)	2	P
			YAV	*Meyer s.n.* (LIL)		
Nassella glabripoda Torres var. *planifolia* Torres	3000	PRE	BEL	*Fabris 4127* (LP)	1	P
Nassella holwayii (Hitchc.) Barkworth**	3560–4200	ALT, PRE, PUN	HUM	*Cabrera 20688a* (LP)	5	P
			RIN	*Cabrera 9340* (LP)		
			TIL	*Werner 623* (BAA)		
			YAV	*Okada 3857* (LP)		
Nassella inconspicua (J. Presl) Barkworth	2000	YUN	BEL	*Burkart s.n.* (SI)	1	P

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Nassella mexicana (Hitchc.) R. W. Pohl	2000–3000	PRE, PUN, YUN	BEL	*Fabris 3949* (LP)	4	P
			SBA	*Fabris 5134* (LP)		
			VGR	*Burkart s.n.* (SI)		
Nassella meyeniana (Trin. & Rupr.) Parodi**	3200–4500	PRE, PUN	COC	*Venturi 9385* (BAA)	8	P
			HUM	*Venturi 8726* (SI)		
			RIN	*Zuloaga 6027* (MO, SI)		
			TUM	*Cabrera 263981/2* (LP)		
Nassella meyeri Torres	2600	PRE	TIL	*Cabrera 19761* (SI)	2	P
Nassella nardoides (Phil.) Barkworth	3500–4600	ALT, PRE, PUN	COC	*Cabezas 17* (LP)	7	P
			HUM	*Fernández 1005* (BAA)		
			RIN	*Schwabe 989* (LP)		
			SUS	*Cabrera 22521* (LP)		
			TIL	*Werner 582* (BAA)		
Nassella neesiana (Trin. & Rupr.) Barkworth	1500–2500	CHA, PRE, YUN	BEL	*Zuloaga 181* (LP)	5	P
			TIL	*Cabrera 13363* (LP)		
			TUM	*Zuloaga 5881* (SI)		
Nassella novari Torres	3000–3400	PRE, PUN	BEL	*Fabris 4043* (LP)	3	P
			TUM	*Cabrera 18524* (LP)		
Nassella nubicola (Speg.) Torres	3200	PRE	TUM	*Cabrera 18390 1/2* (LP)	1	P
Nassella pampagrandensis (Speg.) Barkworth	1990–2900	PRE, PUN	BEL	*Fabris 3950* (LP)	6	P
			SBA	*Fabris 5222* (BAA)		
			TIL	*Fabris 6482* (LP)		
			TUM	*Zuloaga 5883* (SI)		
Nassella parva Torres	1400	CHA	VGR	*Burkart 11689* (SI)	1	P
Nassella pubiflora (Trin. & Rupr.) E. Desv. var. *humilior* Torres**	4000	PUN	YAV	*Cabrera 25711 1/2* (LP)	1	P
Nassella pubiflora (Trin. & Rupr.) E. Desv. var. *levipoda* Torres*	3400–3600	PUN	TUM	*Cabrera 26399* (LP)	3	P
			YAV	*Okada 3862* (LP)		
Nassella pubiflora (Trin. & Rupr.) E. Desv. var. *pubiflora*	3200–4200	PRE, PUN	COC	*Deginani 488* (SI)	14	P
			HUM	*Zuloaga 5953* (SI)		
			TUM	*Nicora 8901* (SI)		
			VGR	*Burkart 11756* (SI)		
			YAV	*Cabrera 15319* (LP)		
Nassella punensis Torres	3450–4500	ALT, PRE, PUN	BEL	*Fabris 4018* (LP)	10	P
			HUM	*Deginani 421* (SI)		
			RIN	*Zuloaga 6034* (SI)		
			SUS	*Cabrera 8768* (LP)		
			TIL	*Werner 584a* (BAA)		
			VGR	*Burkart 11841* (SI)		

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Nassella rupestris (Phil.) Torres	3870	PUN	HUM	*Deginani 433* (SI)	1	P
Nassella tricotoma (Nees) Hack. ex Arechav.	2800	PUN	TUM	*Deginani 363* (SI)	1	P
Nassella tucumana (Parodi) Torres	1500–2500	YUN	BEL	*Zuloaga 158* (LP)	3	P
			SBA	*Cabrera 17330* (LP)		
Nassella yaviensis Torres*	3400–3570	PUN	YAV	*Deginani 585* (SI)	2	P
Piptochaetium indutum Parodi	3450–4000	PUN	HUM	*Zuloaga 5957* (MO, SI)	3	P
			TUM	*Nicora 8804*pp (SI)		
Piptochaetium montevidense (Spreng.) Parodi	1000	CHA	BEL	*Cabrera 27307* (SI)	1	P
Piptochaetium panicoides (Lam.) E. Desv.	3000	PUN	VGR	*Burkart 11620* (SI)	1	P
Piptochaetium stipoides (Trin. & Rupr.) Hack. ex Arechav.	1380	YUN	SBA	*Cabrera 25508* (SI)	1	P
Stipa castellanosii F. A. Roig	2700	PRE	TIL	*Cabrera 11979* (LP)	1	P
Stipa caudata Trin.	2600	PRE	TIL	*Krapovickas 17648* (LIL)	1	P
Stipa durifolia Parodi ex Torres	3600–3700	PRE	HUM	*Soriano 637* (BAA)	2	P
			YAV	*Meyer s.n.* (BAA)		
Stipa frigida Phil.	3920	PUN	SUS	*Hueck 487* (BA)	1	P
Stipa ichu (Ruiz & Pav.) Kunth	1380–3600	PRE, PUN, YUN	BEL	*Fabris 3943* (LP)	8	P
			SBA	*Zuloaga 6374* (SI)		
			TIL	*Cabrera 13924* (LP)		
			TUM	*Zuloaga 5890* (SI)		
			VGR	*Deginani 943* (SI)		
			YAV	*Cabrera 15376* (LP)		
Stipa media (Speg.) Caro	2200–3400	PRE, PUN	TIL	*Zuloaga 6134* (SI)	5	P
			TUM	*Castillón 359b* (LIL)		
			YAV	*Cabrera 24644* (LP)		
Stipa scabrifolia Torres	3750–3810	PUN	COC	*Deginani 552* (SI)	2	P
			SCA	*Deginani 654* (SI)		
Stipa subaristata (Matthei) Caro & E. A. Sánchez	2700–4000	PRE, PUN	HUM	*Ruthsatz s.n.* (MERL)	5	P
			SCA	*Arenas s.n.* (SI)		
			TIL	*Novara 9220* (SI)		
			YAV	*Ruthsatz s.n.* (MERL)		
Tribu Triticeae						
Elymus scabriglumis (Hack.) Á. Löve	2300–3450	PRE, PUN	TIL	*Cabrera 31642* (SI)	3	P
			YAV	*Meyer 14972* (SI)		
Elymus tilcarensis (J. H. Hunz.) Á. Löve*	2460–2700	PRE	TIL	*Hunziker 8082* (BAA, SI)	3	P

Tabla 1. Continuación.

Taxón	Altitud (m)	Provincias fitogeográficas	Dptos	Ejemplar de referencia	#	Ciclo
Hordeum muticum J. Presl	2232–4200	PRE, PUN	COC	*Deginani 506* (SI)	40	P
			HUM	*Zuloaga 5904* (MO, SI)		
			RIN	*Deginani 601* (SI)		
			SCA	*Okada 6722* (SI)		
			TIL	*Cabrera 12022* (BAA)		
			TUM	*Nicora 8886* (SI)		
			YAV	*Meyer 14964* (SI)		
Hordeum pubiflorum Hook. f.	2200–4200	PRE, PUN	HUM	*Burkart 11978* (BAA, SI)	14	P
			TIL	*Zuloaga 3722* (SI)		
			TUM	*Cabrera 15063* (LP)		
			YAV	*Meyer 14915* (LIL)		
Hordeum stenostachys Godr.	2331	PRE	TIL	*Castillón 665* (LIL)	1	P
Hordeum vulgare L.	2430–3600	PRE, PUN	COC	*Cabezas s.n.* (SI-15158)	4	A
			TIL	*Fabris 1859* (BAA)		
			VGR	*Burkart 1701* (SI)		

Resultados

Riqueza y diversidad

Se incorporaron a la base de datos un total de 2330 registros para Jujuy, de los cuales fueron identificadas 373 especies y 23 taxones infraespecíficos, distribuidos en 91 géneros (Tabla 1).

De acuerdo con la clasificación propuesta por GPWG (2001) y CNWG (Judziewicz et al., 2000; Peterson et al., 2001), se hallan 9 subfamilias en la provincia, estando mejor representadas las Pooideae con el 45.04%, las Panicoideae con el 31.55%, y las Chloridoideae con el 19.30% (Tabla 2). Dentro de las Pooideae los géneros con mayor número de especies son *Deyeuxia* Clarion ex P. Beauv. (32 especies), *Nassella* (Trin.) E. Desv. (27), *Festuca* L. (24) y *Poa* L. (18). Las Panicoideae se hallan mejor representadas por los géneros *Paspalum* L. (22), *Setaria* P. Beauv. (16), *Panicum* L. (13), y *Digitaria* Haller (10) y dentro de las Chloridoideae *Eragrostis* Wolf (14), *Muhlenbergia* Schreb. (7), y *Leptochloa* P. Beauv. (6). En relación al número de géneros, el 33% de los mismos corresponden a las Panicoideae y luego le siguen en importancia las Pooideae con el 30% y las Chloridoideae con el 27%. Se registraron 17 tribus en total, de las cuales las subfamilias Pooideae y Panicoideae son las que poseen un mayor número de tribus (5 y 3 tribus respectivamente).

Al examinar el número de géneros y especies por departamento (Tabla 3), se observa que el Dpto. Dr. Manuel Belgrano (BEL) es el que posee la mayor riqueza a nivel genérico (63 géneros) y específico (151 especies). De los 2330 especímenes registrados en Jujuy, 548 (el 23.5%) provienen del mencionado departamento, siendo *Paspalum* (18 especies), *Digitaria* (10), *Eragrostis* (9), *Panicum* (9) y *Nassella* (8), los géneros mejor representados. Los departamentos de Tumbaya (TUM) y Humahuaca (HUM) le siguen en importancia en el número de taxones, con 51 géneros y 122 especies para el primero y 43 géneros y 106 especies para el segundo. En Tumbaya se registraron 293 (el 12.6%) colecciones y en Humahuaca 263 (el 11.3%) colecciones y los géneros mejor representados son *Nassella, Festuca* y *Deyeuxia*. Por otro lado, los departamentos de Rinconada (RIN), Susques (SUS) y Santa Catalina (SCA) registraron el menor número de colecciones, con solamente 90 (el 3.9%), 43 (el 1.8%), y 33 (el 1.4%) colecciones respectivamente. Los géneros más ricos, en estos tres departamentos, son *Deyeuxia, Festuca, Poa* y *Nassella*.

La relación entre el número de especies y el área para cada departamento (Tabla 3), muestra que el Dpto. Dr. Manuel Belgrano posee el 40.37% de las

Tabla 2. Número de tribus, géneros y especies de Poaceae distribuidos por subfamilias en la provincia de Jujuy. (Véase Tabla 1 para nombres de las tribus.)

Subfamilia	N° tribus	N° géneros	N° especies	% especies/familia
Aristidoideae	1	1	6	1.60
Arundinoideae	1	1	1	0.27
Bambusoideae	2	2	2	0.53
Chloridoideae	2	25	72	19.30
Danthonioideae	1	2	4	1.07
Ehrhartoideae	1	2	2	0.53
Panicoideae	3	30	117	31.55
Pharoideae	1	1	1	0.27
Pooideae	5	27	168	45.04
Total	**17**	**91**	**373**	

especies registradas en Jujuy en tan sólo el 4.5% del área total de la provincia, siendo la relación del número de especies por cada 100 km² ligeramente mayor a 6. Contrariamente, Susques, Cochinoca y Rinconada, que suman un área de ca. 45% del total de la provincia, presentan valores muy bajos para tal relación (igual o menor a 0.84%).

Al analizar el número de especies por provincia fitogeográfica, el 43% de las mismas se presentan en la Puna (160 especies), siendo los géneros con mayor número de especies *Deyeuxia* (28), *Nassella* (20), *Festuca* (17) y *Poa* (15). En la Prepuna se relevaron 143 especies (el 38%) y los géneros mejor representados son *Nassella* (17), *Festuca* (11), *Eragrostis* (7), *Deyeuxia* (7) y *Stipa* L. (6). En la provincia Chaqueña se hallaron 142 especies (el 38%) y los géneros con mayor riqueza son *Paspalum* (15), *Setaria* (11), *Digitaria* (10), *Eragrostis* (9) y *Panicum* (8). En las Yungas, con 136 especies (el 36%), los géneros más abundantes son *Paspalum* (19), *Panicum* (9), *Festuca* (8), *Eragrostis* (8) y *Setaria* (6). Un número menor de especies se halló en la provincia Altoandina, con sólo el 11% del número total de especies (40), y entre los géneros con mayor número de especies están *Deyeuxia* (10), *Festuca* (6) y *Nassella* (4).

Los valores obtenidos para el índice de Chao (1984) indican que el número de especies aquí registrado es muy próximo al número de especies estimado para la mayor parte del área de la provincia. Esto se desprende de observar que para 12 departamentos de los 15 que posee Jujuy, los valores del índice de Chao superan el 70% (Tabla 4). A diferencia de esto, los departamentos de Santa Catalina, San Antonio, y Susques arrojaron un porcentaje mucho menor (menor a 55%).

Tabla 3. Número de géneros y especies de Poaceae distribuidos por departamento en la provincia de Jujuy. (Véase Tabla 1 para abreviaturas de los departamentos.)

Departamento	N° géneros	N° especies	% especies	Superficie (km²)	N° spp/100 km²
BEL	63	151	40.37	2384	6.33
COC	23	44	11.76	7837	0.56
ECA	22	52	13.90	912	5.7
HUM	43	106	28.34	3792	2.8
LED	39	83	22.19	3249	2.55
RIN	22	54	14.44	6407	0.84
SAN	7	7	1.87	690	1.01
SBA	33	71	18.98	4448	1.6
SCA	21	33	8.82	2960	1.11
SPE	26	59	15.78	2150	2.74
SUS	14	23	6.15	9199	0.25
TIL	32	69	18.45	1845	3.74
TUM	51	122	32.62	3442	3.54
VGR	33	66	17.65	962	6.86
YAV	29	73	19.52	2942	2.48
Total	**91**	**373**			

Tabla 4. Número de especies registradas por departamentos y número de especies estimadas por departamento, calculado según el índice de Chao (1984). (Véase Tabla 1 para abreviaturas de los departamentos.)

Departamento	N° especies registradas	N° especies estimadas	% representado
BEL	151	167	90
COC	44	58	76
ECA	52	70	74
HUM	106	139	76
LED	83	106	78
RIN	54	77	70
SAN	7	13	54
SBA	71	93	76
SCA	33	76	43
SPE	59	82	72
SUS	23	51	45
TIL	69	92	75
TUM	122	154	79
VGR	66	99	70
YAV	73	104	70

DISTRIBUCIÓN ALTITUDINAL DE LAS ESPECIES

Sobre los datos presentados en la Tabla 1, puede observarse que el mayor número de especies se distribuyen principalmente entre los 600 y 3400 m de altitud (Fig. 3), alcanzando los 5170 m una especie de la tribu Poeae, *Anthochloa lepidula*. Dentro de las subfamilias Bambusoideae y Pharoideae, *Chusquea lorentziana*, *Olyra fasciculata* y *Pharus lappulaceus* se hallan en las regiones más bajas, en área de Yungas entre los 460 y 1700 m. *Chusquea lorentziana* crece preferentemente en lugares rocosos, sombríos y húmedos, mientras que *O. fasciculata* y *P. lappulaceus* son frecuentes en bordes o interior de selvas, en lugares sombríos y húmedos.

Las especies de la subfamilia Ehrhartoideae presentan mayor preponderancia entre los 300 y 2000 m, en las provincias Chaqueña y de las Yungas, generalmente habitan en ambientes bajos, a menudo modificados, húmedos e inundables o junto a cursos de agua.

La subfamilia Panicoideae presenta un amplio

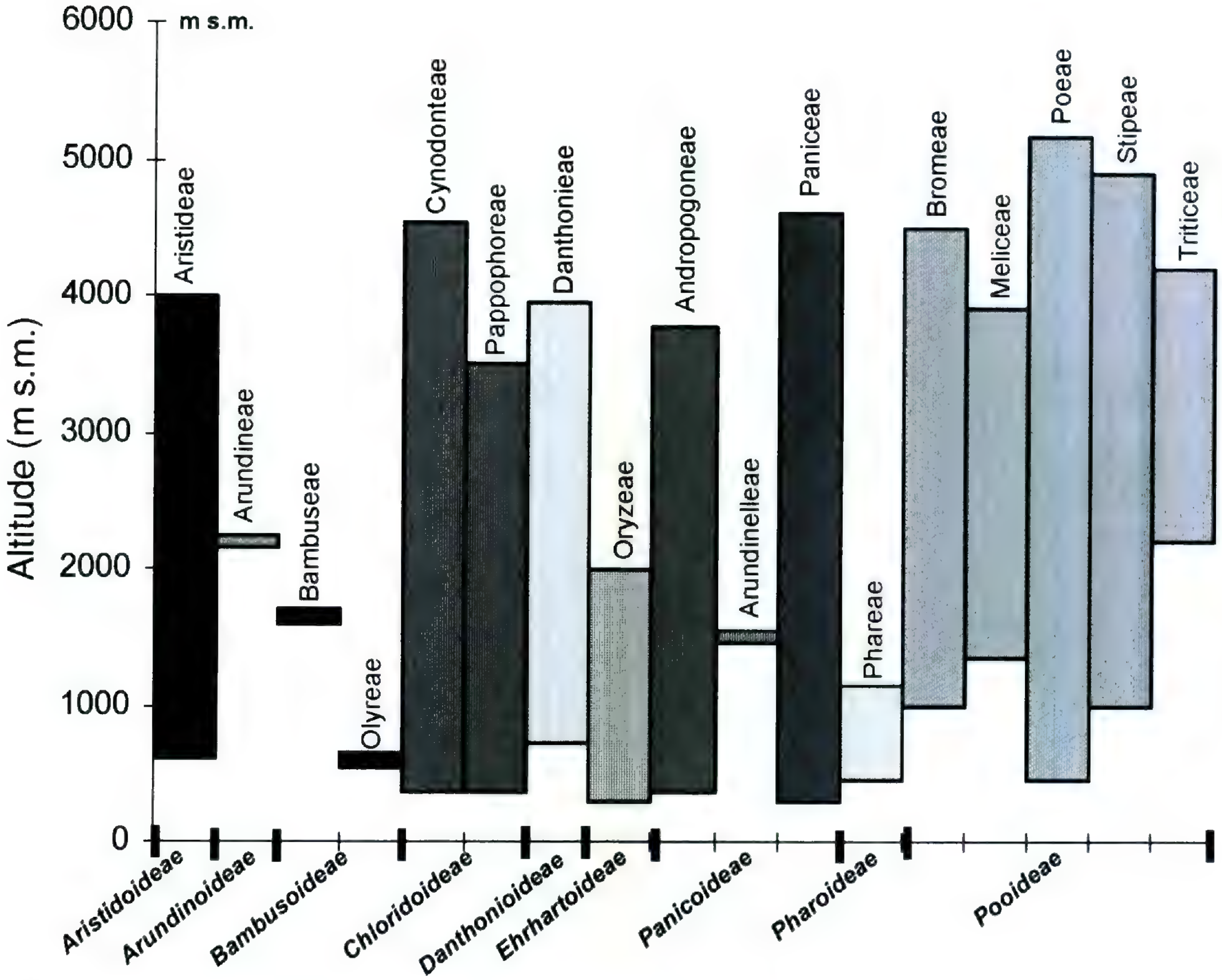

Figura 3. Distribución altitudinal de las tribus de Poaceae de Jujuy.

rango de altitud desde los 330 m hasta 4600 m, con una mayor concentración de especies entre los 500 m y los 2500 m. Esta subfamilia se concentra en las provincias Chaqueña, de la Prepuna y de las Yungas, con unas pocas especies pertenecientes a los géneros *Digitaria* (*D. californica*), *Elionurus* Humb. & Bonpl. ex Willd. (*E. muticus*), *Panicum* (*P. chloroleucum*), *Bothriochloa* Kuntze (*B. saccharoides*) y *Pennisetum* Rich. (*P. chilense*) que se hallan en la Puna, superando los 3000 m.

La subfamilia Arundinoideae, con *Phragmites australis*, es común a 2000 m de altura en la Quebrada de Humahuaca, siendo frecuente en suelos húmedos, anegados, o en borde de canales de riego, ríos y arroyos.

Las especies de la subfamilia Aristidoideae mostraron una tendencia a concentrarse por encima de los 2800 m, en las provincias Altoandina, de la Prepuna y Puna. *Aristida pedroensis* fue la única especie de esta tribu registrada a los 600 m s.m., en la provincia Chaqueña.

La mayor riqueza de las especies de la subfamilia Chloridoideae se halló entre los 740 m y los 3900 m, con especies de *Distichlis* Raf., *Leptochloa*, *Muhlenbergia* y *Munroa* Torr., de la tribu Cynodonteae, que superan los 4000 m s.m.

La subfamilia Danthonioideae se distribuye preferentemente por encima de los 2000 m hasta los 3950 m, en la Prepuna y Puna, a excepción de *Lamprothyrsus hieronymi*, especie que se extiende desde los 720 m hasta los 3500 m en las Yungas, alcanzando los campos de altura y creciendo sobre laderas de montaña, en paredones pedregosos o rocosos.

Las especies de la subfamilia Pooideae se registraron, en su mayor parte, entre los 1000 y 5170 m, mientras que algunos géneros como *Deyeuxia*, *Festuca*, *Poa*, *Anatherostipa* (Hack. ex Kuntze) Peñailillo, *Jarava* Ruiz & Pav., *Nassella* y *Stipa*, incluyen varias especies por encima de los 3000 m, predominando en la Prepuna y Puna. Por el contrario, *Chaetotropis elongata*, *Polypogon monspeliensis* y *P. viridis* alcanzan altitudes por debajo de los 1000 m en las provincias Chaqueña y de las Yungas.

ESPECIES ENDÉMICAS E INTRODUCIDAS

Se hallaron 10 especies y 2 variedades endémicas en la provincia de Jujuy (Tabla 1, Fig. 1). *Aristida pedroensis*, *Deyeuxia cabrerae* var. *minima* y *Poa grisebachii* sólo son conocidas por colecciones del material tipo. *Aristida pedroensis* crece en cercanías de la ciudad de San Pedro, en la provincia Chaqueña, a 600 m s.m. *Poa grisebachii* es endémica de Santa Catalina y habita en lugares húmedos y protegidos de la Puna a 3500 m de altura. Finalmente, *Deyeuxia cabrerae* var. *maxima* fue coleccionada en Cochinoca, en el Co. Huancar, Abra Pampa, a 3500 m de altura.

Cabe destacar que las especies endémicas se encuentran, en buena parte, entre los 2400 y los 4000 m, en correspondencia con las provincias fitogeográficas de la Prepuna y Puna; solo uno de los registros de las especies endémicas se halla en la provincia Altoandina (*Anatherostipa henrardiana*), otro en la provincia Chaqueña (*Aristida pedroensis*) y *Festuca superba* en la provincia de las Yungas.

En relación al número de especies restringidas a la provincia se hallaron 21 taxones (Tabla 1), los que están presentes en áreas vecinas de Bolivia o Chile y sólo llegan en la Argentina a la provincia de Jujuy.

Crecen en Jujuy un total de 28 especies introducidas (Tabla 1), lo que representa el 7.5% del total de la flora agrostológica. El mayor número de especies introducidas se halló en la región Chaqueña (19) y en las Yungas (11).

ANÁLISIS FLORÍSTICO

Los valores de comparación específica en los 15 departamentos muestran bajos niveles de similitud entre ellas. La similitud más alta se halla entre Humahuca y Yavi, con 47 especies en común y un coeficiente de 0.525, seguida por El Carmen y San Pedro, compartiendo 29 especies y un coeficiente de 0.522. El análisis de agrupamiento de la composición de especies por departamento (Fig. 4), permite reconocer diversas relaciones de similitud entre los departamentos de Jujuy. El Carmen y San Pedro tienen la similitud más alta, y este grupo se une con los departamentos de Dr. M. Belgrano, Santa Bárbara y Ledesma. Por otro lado, Humahuaca y Yavi presentan mayor similitud entre sí y muestran mayor relación con Cochinoca y Rinconada y a su vez éstos con Santa Catalina. Los departamentos de Tilcara y Tumbaya muestran también mayor afinidad con éste último grupo.

La comparación específica por provincias fitogeográficas indica valores de similitud altos entre la Prepuna y la Puna, compartiendo 78 especies y un coeficiente de 0.515. A continuación, la provincia Altoandina y de la Puna poseen 44 especies en común y un coeficiente de similitud de 0.438. En la Figura 5 se muestra el diagrama de agrupamiento de la composición de especies por provincias fitogeográficas. La Prepuna y la Puna tienen la mayor similitud y ambas se unen luego con la provincia Altoandina, y por último se conectan con las

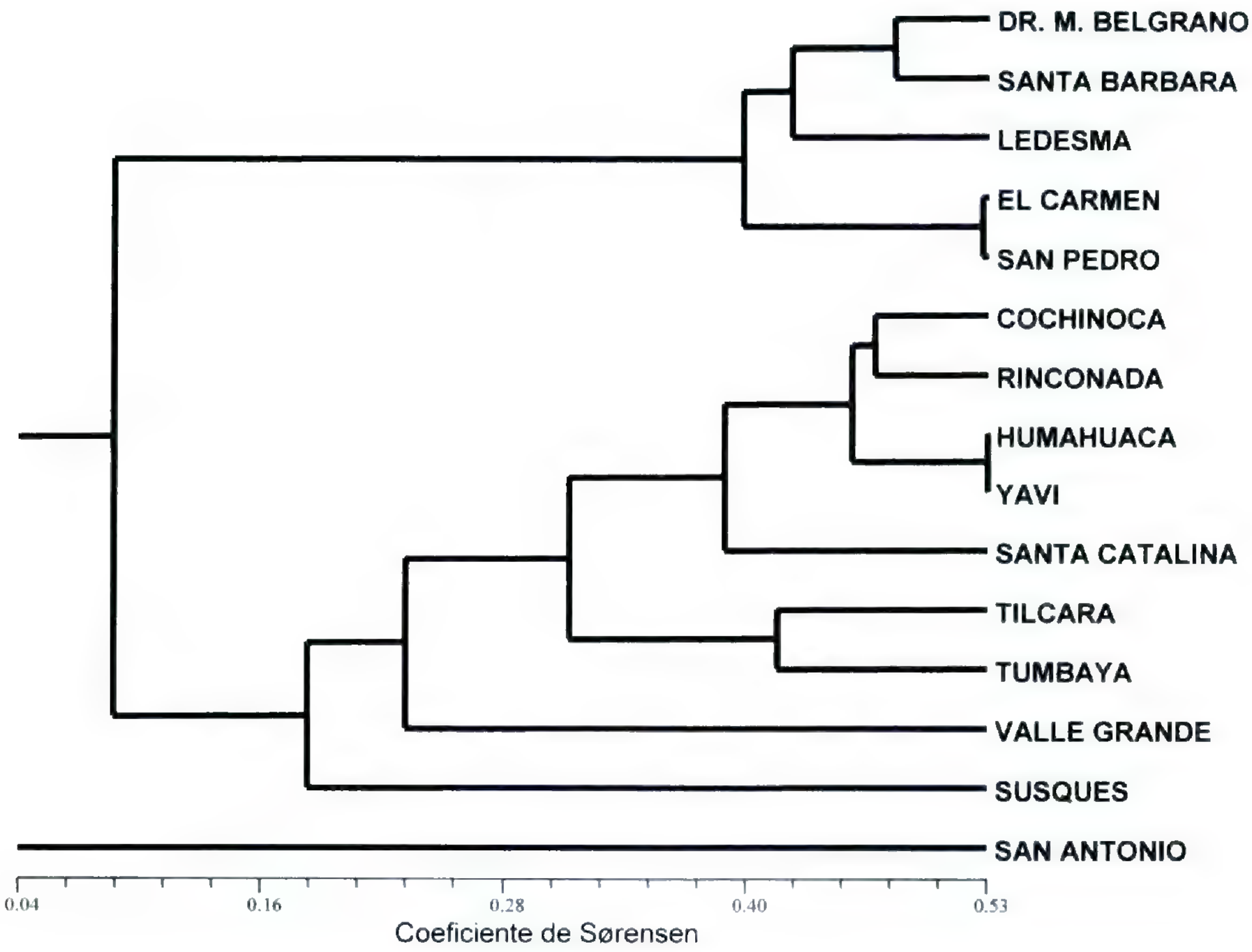

Figura 4. Diagrama de agrupamiento de la composición de especies en diferentes departamentos de la provincia de Jujuy.

provincias fitogeográficas Chaqueña y de las Yungas en niveles más bajos de similitud.

Discusión

Riqueza de taxones

Según Cabrera (1957), la notable diversidad de la flora del noroeste argentino se debe al levantamiento de la Cordillera de los Andes durante el Terciario. Este hecho, seguido de movimientos tectónicos y fenómenos de vulcanismo que se prolongaron hasta el Cuaternario, generaron un clima inadecuado para la flora tropical y subtropical que originalmente se desarrollaba en esta zona. Estas profundas modificaciones en la fisiografía y el clima, diversificaron los ambientes que bajo diversos

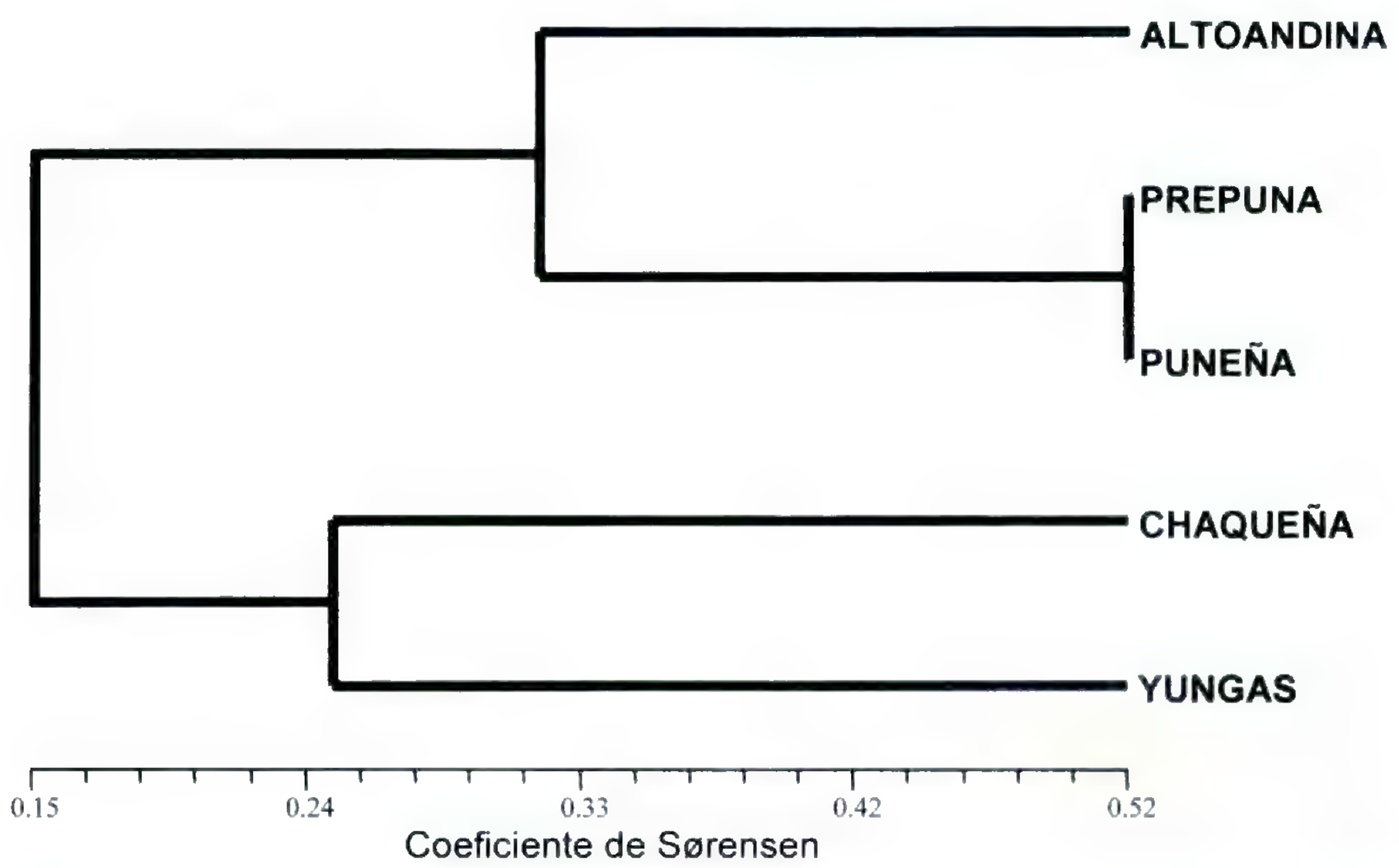

Figura 5. Diagrama de agrupamiento de la composición de especies en diferentes provincias fitogeográficas de Jujuy.

Tabla 5. Número de géneros y especies de Poaceae registrados en diferentes provincias o regiones de Argentina y países limítrofes. Datos tomados de Burkart (1969); Cabrera (1970); Nicora (1978); Steibel et al. (1997); Renvoize (1998); base IRIS©.

Provincia/Región	N° géneros	N° especies	Superficie (km²)	N° spp/10³km²
Jujuy	91	373	53219	7
Entre Ríos	95	328	78781	4
Buenos Aires	103	375	307571	1
Patagonia	77	379	786983	0.4
La Pampa	77	238	143440	1
Bolivia (Tarija-Potosí-Chuquisaca)	87	309	207365	1.5
Chile (II Región)	25	68	125000	0.5

mecanismos de evolución y selección podrían haber generado nuevas formas mejor adaptadas a las nuevas condiciones.

Los resultados del presente análisis mostraron que la riqueza específica de la familia Poaceae en la provincia de Jujuy es notoria y supera en gran escala a otras regiones de Argentina, más amplias pero menos diversas geográficamente (véase Tabla 5). Los mayores valores de riqueza se concentraron en la parte oriental de Jujuy, donde el relieve es más accidentado, con grandes variaciones climáticas y edáficas, en una superficie relativamente restringida. Dentro de esta zona, el departamento Dr. Manuel Belgrano fue el que presentó el mayor grado de riqueza a nivel específico. El rango altitudinal de este departamento es muy amplio, con al-

Tabla 6. Número de especies de cada taxón de Poaceae en las provincias fitogeográficas de Jujuy. El denominador indica el porcentaje relativo de composición de especies de la subfamilia en cada provincia fitogeográfica. (Véase Tabla 1 para abreviaturas de las provincias fitogeográficas.)

Taxón	ALT	CHA	PRE	PUN	YUN
Subfam. Aristidoideae	1/11	1/11	2/22	5/56	—
Aristideae	1	1	2	5	—
Subfam. Arundinoideae	—	—	1/100	—	—
Arundineae	—	—	1	—	—
Subfam. Bambusoideae	—	—	—	—	2/100
Bambuseae	—	—	—	—	1
Olyreae	—	—	—	—	1
Subfam. Chloridoideae	8/6	42/30	41/30	27/20	19/14
Cynodonteae	8	39	38	25	19
Pappophoreae	—	3	3	2	—
Subfam. Danthonioideae	—	—	3/60	1/20	1/20
Danthonieae	—	—	3	1	1
Subfam. Ehrhartoideae	—	1/34	—	—	2/66
Oryzeae	—	1	—	—	2
Subfam. Panicoideae	1/1	88/47	22/12	4/2	70/38
Andropogoneae	—	16	6	1	9
Arundinelleae	—	—	—	—	1
Paniceae	1	72	16	3	60
Subfam. Pharoideae	—	—	—	—	1/100
Phareae	—	—	—	—	1
Subfam. Pooideae	30/11	10/3	74/27	123/44	41/15
Bromeae	1	1	3	4	3
Meliceae	—	—	2	1	1
Poeae	20	5	33	78	30
Stipeae	9	4	30	36	7
Triticeae	—	—	6	4	—

turas de hasta 6200 m s.m. en la serranía del Chañi, y localidades que no alcanzan los 300 m s.m., como por ejemplo en proximidades del paraje denominado "El Pongo." Esto hace que dentro de los límites del departamento se hallen representadas las 5 provincias fitogeográficas presentes en Jujuy.

Otro factor importante a tener en cuenta, es que la zona oriental de Jujuy tiene posibilidades de acceso en casi toda su extensión a través de la ruta Nacional 9 y de la red ferroviaria (aunque ésta última no está habilitada en la actualidad). Estos accesos están trazados entre cordones montañosos, siguiendo mayormente el curso de la Quebrada de Humahuaca. La presencia de las mencionadas rutas de acceso, podrían sugerir que en algunos casos los valores de riqueza específica pudiesen estar sobrestimados ya que por razones de eficiencia, logística y conveniencia, las colecciones tienden a hacerse siguiendo rutas que conectan ciudades importantes (Hijmans et al., 2000). Es probable que las rutas de acceso en la zona oriental de Jujuy hayan facilitado el número de colecciones botánicas en dicha área. De esta forma, los departamentos de Yavi, Humahuaca, Tumbaya, Tilcara, Valle Grande, Dr. Manuel Belgrano, Ledesma y Santa Bárbara fueron los que mostraron valores del Índice de Chao igual o superior al 70% (Tabla 4), indicando que se cuenta con una gran proporción del número real de especies. Sin embargo, es importante resaltar que zonas muy accesibles, como San Pedro y El Carmen, y otras de difícil acceso, como Rinconada y Cochinoca, presentaron igualmente baja riqueza específica, pero un valor confiable del número de especies estimado (Índice de Chao superior o igual al 70%). Contrariamente, San Antonio, localizado relativamente próximo a San Salvador de Jujuy, ciudad capital de la provincia, cuenta con muy baja riqueza (Índice de Chao 54%) probablemente relacionada a que esta zona se halla altamente modificada por factores antrópicos.

Los departamentos de Susques, Cochinoca, Santa Catalina y Rinconada, ubicados en la zona occidental de Jujuy, presentaron valores de riqueza específica comparativamente más bajos. Esta zona representa casi el 50% del área total y posee las condiciones más desfavorables de suelo (salinos, rocosos, etc.), humedad ambiental muy baja, clima frío y seco característico de las provincias fitogeográficas Puneña y Altoandina, alcanzando mínimas de −20°C en invierno y lluvias que no superan los 200–300 mm anuales, y con escasa vegetación.

Los datos obtenidos en el presente trabajo permiten concluir que la zona oriental de Jujuy, la cual es muy heterogénea en lo que al relieve y clima se refiere, concentra la mayor diversidad de taxones de Poaceae. Esta variación espacial tan marcada ofrecería más oportunidades para que especies con diferentes grados de tolerancia puedan establecerse, ya que aumenta la disponibilidad de nichos ecológicos (Aarsen, 1992). Contrariamente, la zona occidental de la provincia presenta menor grado de diversidad. Esto podría deberse a que las variables climáticas más extremas restringen la presencia de especies debido al mayor costo adaptativo que requieren las mismas para establecerse (Begon et al., 1990).

RELACIÓN CON LA FLORA DE OTRAS ÁREAS DE ARGENTINA Y CON PAÍSES LIMÍTROFES

De la comparación de la flora agrostológica de diferentes áreas de Argentina con nuestra área de estudio (Tabla 5), se desprende que la Provincia de Jujuy (53219 km²) posee un número de especies (373) similar a los presentes en otras áreas de mayor superficie, como es el caso de la Patagonia (379 especies en 786983 km²) o la Provincia de Buenos Aires (375 especies en 307571 km²). Asimismo, en Jujuy se hallan representados el 31% de las especies y el 52% de géneros de Poaceae conocidos para la Argentina (Zuloaga et al., 1994, 1999). La relación entre el número de especies y el área muestreada es de 7 especies/10^3 km² en Jujuy. Esta relación es comparativamente mayor a la hallada en otras regiones intensamente muestreadas de Argentina, como las provincias de La Pampa, Entre Ríos y de Buenos Aires, o la Patagonia (Burkart, 1969; Cabrera, 1970; Nicora, 1978; Steibel et al., 1997) con valores relativamente más bajos en relación al número de especies/área (Tabla 5). Con las floras previamente descriptas, la flora de Poaceae de Jujuy comparte especies de amplia distribución de acuerdo al siguiente detalle: con La Pampa 100 especies, con la Flora de Buenos Aires 142 especies, con la provincia de Entre Ríos 130 especies, y un total de 67 especies con las Poaceae de la Flora Patagónica. Si consideramos la relación de la flora con la provincia vecina de Salta, existen en total 298 especies en común entre ambas provincias, con 401 especies presentes de Poaceae en Salta.

Al comparar las Poaceae de la flora de Jujuy con los países limítrofes se observó que la provincia de Jujuy presenta una mayor afinidad con las gramíneas de Bolivia (Renvoize, 1998). Si se consideran los departamentos del sur de Bolivia, Tarija, Chuquisaca y Potosí, con un total de 207365 km², se encuentran en ellos un total de 309 especies, de las cuales 205 son compartidas con Jujuy, o sea el

66.34% de las especies. Las subfamilias mejor representadas son las Pooideae con 121 especies, las Panicoideae con 92 especies, y las Chloridoideae con 76 especies. La relación número de especies/área en el sur de Bolivia es comparativamente menor a la hallada en Jujuy, con 1.5 especies/10^3 km^2. Renvoize (1998), al analizar la distribución de las especies de Poaceae en Bolivia, señala a los departamentos de Tarija, Chuquisaca y Potosí como áreas poco coleccionadas y que requieren futuras exploraciones, lo que podría eventualmente incrementar la relación entre el número de especies y el área. En Bolivia el departamento de Potosí incluye, desde el punto de vista fitogeográfico, vegetación de Puna y Altoandina, con predominio de especies de la subfamilia Pooideae y, en menor medida, de géneros de Chloridoideae (Beck, 1998). A su vez, los departamentos de Chuquisaca y Tarija poseen, de acuerdo a Beck (1998), una vegetación predominante de bosque tucumano-boliviano (Yungas), bosque serrano chaqueño y de valles secos interandinos y cabecera de valle, en donde dominan elementos de las subfamilias Bambusoideae, Chloridoideae y Panicoideae, con una menor representación de la subfamilia Pooideae.

Existe una menor afinidad de las gramíneas de Jujuy con las gramíneas de Chile (Marticorena & Quezada, 1985; IRIS©), país con el cual comparte un total de 151 taxones, lo que representa el 25% de las especies registradas. Al relacionar a la flora agrostológica de Jujuy con áreas vecinas de Chile, en la II Región, con 125000 km^2, se encuentran un total de 68 especies de Poaceae, con 17 especies y 2 variedades endémicas; predominan las Pooideae (49 especies), seguidas por las Chloridoideae (15), con solo 2 representantes de las Panicoideae y 1 especie de Arundinoideae). Existen 30 especies compartidas con Jujuy, lo que representa un 8% de taxones compartidos; los géneros que comparten un mayor número de especies pertenecen a las Pooideae y son *Deyeuxia*, *Festuca*, *Nassella* y *Poa*. Esta menor afinidad, y el hecho de que se encuentren en Chile una menor cantidad de especies, se debe al aislamiento impuesto por la Cordillera de los Andes y al hecho de que la II Región, limítrofe con Jujuy, se ubica en la zona árida del oeste de Sudamérica. En esta área la extrema aridez impone fuertes restricciones al crecimiento de las plantas (Marticorena et al., 1998); esto se ve reflejado en la relación entre el número de especies y el área muestreada con un valor estimado de 0.5 especies/10^3 km^2. Esta relación es claramente menor a la hallada en Jujuy, y similar a la presente en la Patagonia, donde la mayor parte de la superficie corresponde a una región árida con intensos vientos del oeste y muy bajas temperaturas invernales.

ESPECIES ENDÉMICAS Y NATIVAS

Al comparar el nivel de endemismo de las Poaceae (10 especies) con los endémicos de otras familias de plantas vasculares bien representadas en la provincia (Asteraceae: 19 especies; Fabaceae: 6 especies; Solanaceae: 6 especies), resulta claro que estos valores guardan directa relación con el número de endémicos en el país: Asteraceae, con un total de 370 especies endémicas; Poaceae, con 192 especies endémicas; Fabaceae, con 154 especies endémicas; y Solanaceae, con un total de 101 especies endémicas. A la vez, si consideramos las provincias biogeográficas presentes en Jujuy y en el noroeste de la Argentina (abarcando las provincias políticas de Jujuy, Salta, Tucumán y Catamarca), el nivel de endemismo es el siguiente: Asteraceae (71 especies), Poaceae (31), Solanaceae (19) y Fabaceae (13).

Al considerar los taxones de Poaceae presentes en Jujuy y en otras regiones de la Argentina, excepción hecha de las especies endémicas y/o exclusivas para Jujuy, un total de 100 especies están restringidas a las provincias fitogeográficas de las Yungas, Chaco, Prepuna, Puna y región Altoandina en el noroeste argentino; esta región incluye a las provincias de Jujuy, Salta, Tucumán y Catamarca. Otras 39 especies se distribuyen a lo largo de la Cordillera y Precordillera, llegando hasta Mendoza y San Juan.

En relación con regiones vecinas de los países limítrofes, el porcentaje de endemismo es más elevado en el norte de Chile, con un total de 68 especies presentes en la II Región y 17 especies y 2 variedades endémicas, lo que representa un porcentaje de endemismo del 25%. Por otra parte, en el sur de Bolivia se encuentran, tal como se mencionó anteriormente, 309 especies de Poaceae, siendo 6 de las mismas endémicas para esa región, representando el 2% de endemismo para los 3 departamentos analizados.

PROVINCIAS BIOGEOGRÁFICAS

Cabrera (1976) y Cabrera y Willink (1973) ubican a la Provincia de la Prepuna dentro del Dominio Chaqueño y, dentro de este dominio, señalan que sus relaciones más cercanas son con la Provincia Chaqueña. Recientemente, Morrone (1999) publicó un nuevo esquema biogeográfico para América del Sur, señalando que la Prepuna debe incluirse en la Región Andina, junto con las Provincias de la Puna y Altoandina entre otras. El

presente análisis, en el que la Prepuna se halla claramente relacionada con la Provincia de la Puna y la Provincia Altoandina, fundamentalmente a través de especies de la subfamilia Pooideae, avala el esquema propuesto por Morrone (1999). Asimismo, se observa una clara relación entre las provincias de las Yungas y Chaqueña, a través de numerosos taxones comunes, principalmente de las subfamilias Panicoideae y Chloridoideae.

RELACIÓN ENTRE LAS PROVINCIAS BIOGEOGRÁFICAS Y LAS SUBFAMILIAS DE POACEAE

La distribución de las gramíneas, de acuerdo con el tipo fotosintético que presentan y a la clasificación en subfamilias, se encuentra relacionada con la temperatura, precipitaciones y exposición solar (Hattersley, 1983, 1987); estos factores inciden en el ordenamiento de las Poaceae en la provincia de Jujuy de acuerdo con el siguiente detalle:

Las subfamilias Bambusoideae y Pharoideae se presentan exclusivamente en la provincia de las Yungas, habitando frecuentemente en bordes de selvas, en lugares sombríos y húmedos; una distribución similar se presenta en la subfamilia Ehrhartoideae, con dos especies en la provincia de las Yungas, una de ellas, *Leersia hexandra,* llega a la provincia Chaqueña. Esta distribución, y la preferencia de estos taxones por lugares húmedos y sombríos, está de acuerdo con el hecho de que estas subfamilias incluyen plantas C_3 o non Kranz. A la vez, es llamativo el bajo número de especies de la subfamilia Bambusoideae, la que se halla ricamente representada en Bolivia y en el sur de Brasil, Paraguay y noreste de la Argentina.

La subfamilia Chloridoideae posee un mayor número de especies en las provincias Chaqueña y de la Prepuna; dentro de la subfamilia hay en estas provincias un mayor número de taxones de la tribu Cynodonteae; no obstante, esta tribu también se halla bien representada en la Puna y en las Yungas. Ésta subfamilia incluye taxones que preferentemente habitan en lugares áridos a semiáridos y con relativa sequía; son plantas Kranz o C_4 y la distribución que presentan en Jujuy guarda relación directa con el tipo fotosintético de la subfamilia.

La subfamilia Panicoideae posee una mayor riqueza en las provincias Chaqueña y de las Yungas, en particular en lo que respecta a la tribu Paniceae. Algunas especies están presentes en la Prepuna y son raras las especies que llegan a alturas mayores en la Puna (*Bothriochloa saccharoides, Digitaria californica, Panicum chloroleucum* y *Pennisetum chilense*). La tribu Andropogoneae, que incluye en su totalidad a plantas Kranz, posee varios géneros presentes en la provincia Chaqueña, como *Hemarthria* R. Br., *Heteropogon* Pers., *Imperata* Cyrillo, *Schizachyrium* Nees, *Rottboellia* L.f., *Sorghastrum* Nash, *Sorghum* Moench y *Themeda* Forssk. Géneros Kranz mayoritariamente chaqueños de las Paniceae son *Cenchrus* L., *Setaria* y *Urochloa* P. Beauv. Dentro de esta última tribu se encuentran géneros Kranz y non Kranz con una distribución variable en la provincia Chaqueña y de las Yungas; dentro de los géneros non Kranz, de la subtribu Panicoideae, que habitan en las Yungas se puede mencionar *Arundinella* Raddi (tribu Arundinelleae) y *Echinolaena* Desv., *Ichnanthus* P. Beauv., *Lasiacis* Hitchc., *Oplismenus* P. Beauv. y *Pseudechinolaena* Stapf (tribu Paniceae).

Las Pooideae poseen claramente una mayor diversidad hacia el oeste de Jujuy, lo que está de acuerdo con el hecho de ser la subfamilia enteramente non Kranz; de allí la preferencia, en términos generales, por ambientes fríos y a altitudes relativamente elevadas. Ejemplos de géneros que se encuentran exclusivamente en las provincias de la Prepuna y la Puna son *Alopecurus* L., *Anthochloa* Nees & Meyen, *Dielsiochloa* Pilg., *Dissanthelium* Trin., *Elymus* L., *Hordeum* L. y *Lolium* L. Las tribus mejor representadas son las Stipeae y Poeae con una distribución predominante de sus especies en las provincias Altoandina, Prepuna, y Puna; también se hallan en las provincia de las Yungas y Chaqueña.

Las Arundinoideae se hallan presentes con una única especie, *Phragmites australis,* en la Prepuna. La subfamilia Danthonioideae se distribuyen preferentemente en la Puna y Prepuna, con tres especies del género *Cortaderia* Stapf, y una especie del género *Lamprothyrsus* Pilg. exclusiva de las Yungas. Finalmente, la subfamilia Aristidoideae, con una única tribu, presenta mayor riqueza específica en la Puna (Tabla 6).

Esta correlación de gramíneas non Kranz a mayores altitudes, lo que se presenta mayormente en la subfamilia Pooideae, y de especies Kranz, a altitudes menores y en ambientes secos y semiáridos a áridos, fundamentalmente elementos de las subfamilias Chloridoideae y Panicoideae, está de acuerdo con resultados previos para Poaceae del centro de la Argentina (Cabido et al., 1997).

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Correspondence

Submissions should be addressed to:

Beth Parada
Managing Editor
Annals of the Missouri Botanical Garden
Missouri Botanical Garden Press
P.O. Box 299, St. Louis, MO 63166-0299 U.S.A.

Managing Editor
Annals of the Missouri Botanical Garden
(Street address)
Missouri Botanical Garden Press
Monsanto Center
4500 Shaw Blvd.
St. Louis, MO 63110-2291 U.S.A.
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Volume 92
2005

ALISCIONI, SANDRA S. (see Osvaldo Morrone, Sandra S. Aliscioni & Fernando O. Zuloaga) 595

AL-SHEHBAZ, IHSAN A. (see Klaus Mummenhoff, Ihsan A. Al-Shehbaz, Freek T. Bakker, H. Peter Linder & Andreas Mühlhausen) 400

AMATO, GEORGE (see Paul Goldstein, Yael Wyner, Phaedra Doukakis, Mary G. Egan, George Amato, Howard Rosenbaum & Rob DeSalle) 12

BAKKER, FREEK T. (see Klaus Mummenhoff, Ihsan A. Al-Shehbaz, Freek T. Bakker, H. Peter Linder & Andreas Mühlhausen) 400

BARKER, NIGEL P. A Review and Survey of Basicarpy, Geocarpy, and Amphicarpy in the African and Madagascan Flora 445

BARKER, N. P. (see R. J. McKenzie, J. Samuel, E. M. Muller, A. K. W. Skinner & N. P. Barker) 569

BARTHLOTT, WILHELM (see Colin J. McClean, Jon C. Lovett, Wolfgang Küper, Lee Hannah, Jan Henning Sommer, Wilhelm Barthlott, Mette Termansen, Gideon F. Smith, Simon Tokumine & James R. D. Taplin) 139

BERNHARDT, PETER (see Peter Goldblatt, John C. Manning & Peter Bernhardt) 268

BORSCH, THOMAS (see Kai Müller & Thomas Borsch) 66

BOUFFORD, DAVID E. (see Ze-Long Nie, Jun Wen, Zhi-Jian Gu, David E. Boufford & Hang Sun) 275

CANO, MARÍA J. (see Juan A. Jiménez, Rosa M. Ros, María J. Cano & Juan Guerra) 225

CARR, DAVID E. (see Michele R. Dudash, Courtney J. Murren & David E. Carr) 36

CHIANG, TZEN-YUH (see Kuo-Hsiang Hung, Tsai-Wen Hsu, Barbara A. Schaal & Tzen-Yuh Chiang) 52

DELPRETE, PIERO G., MICHAEL NEE & JIFKE KOEK-NOORMAN. Resurrection and Revision of *Patima* (Rubiaceae, Cinchonoideae, Hamelieae) 103

DENHAM, SILVIA SUYAI. Revisión Sistemática del Subgénero *Harpostachys* de *Paspalum* (Poaceae: Panicoideae: Paniceae) 463

DESALLE, ROB (see Paul Goldstein, Yael Wyner, Phaedra Doukakis, Mary G. Egan, George Amato, Howard Rosenbaum & Rob DeSalle) 12

DOUKAKIS, PHAEDRA (see Paul Goldstein, Yael Wyner, Phaedra Doukakis, Mary G. Egan, George Amato, Howard Rosenbaum & Rob DeSalle) 12

DUDASH, MICHELE R., COURTNEY J. MURREN & DAVID E. CARR. Using *Mimulus* as a Model System to Understand the Role of Inbreeding in Conservation: Genetic and Ecological Approaches 36

EDWARDS, T. J. (see C. J. Potgieter & T. J. Edwards) 254

EGAN, MARY G. (see Paul Goldstein, Yael Wyner, Phaedra Doukakis, Mary G. Egan, George Amato, Howard Rosenbaum & Rob DeSalle) 12

Finot, Víctor L., Paul M. Peterson, Fernando O. Zuloaga, Robert J. Soreng & Oscar Matthei. A Revision of *Trisetum* (Poaceae: Pooideae: Aveninae) in South America 533

Frodin, David G. (see Gregory M. Plunkett, Porter P. Lowry II, David G. Frodin & Jun Wen) 202

Gereau, Roy E. (see Charlotte M. Taylor, Roy E. Gereau & Gretchen M. Walters) 360

Goldblatt, Peter, John C. Manning & Peter Bernhardt. The Floral Biology of *Melasphaerula* (Iridaceae: Crocoideae): Is This Monotypic Genus Pollinated by March Flies (Diptera: Bibionidae)? 268

Gottschling, Marc, James S. Miller, Maximilian Weigend & Hartmut H. Hilger. Congruence of a Phylogeny of Cordiaceae (Boraginales) Inferred from ITS1 Sequence Data with Morphology, Ecology, and Biogeography 425

Goldstein, Paul, Yael Wyner, Phaedra Doukakis, Mary G. Egan, George Amato, Howard Rosenbaum & Rob DeSalle. Theory and Methods for Diagnosing Species and Populations in Conservation 12

Gu, Zhi-Jian (see Ze-Long Nie, Jun Wen, Zhi-Jian Gu, David E. Boufford & Hang Sun) 275

Guerra, Juan (see Juan A. Jiménez, Rosa M. Ros, María J. Cano & Juan Guerra) 225

Hannah, Lee (see Colin J. McClean, Jon C. Lovett, Wolfgang Küper, Lee Hannah, Jan Henning Sommer, Wilhelm Barthlott, Mette Termansen, Gideon F. Smith, Simon Tokumine & James R. D. Taplin) 139

Hilger, Hartmut H. (see Marc Gottschling, James S. Miller, Maximilian Weigend & Hartmut H. Hilger) 425

Hoch, Peter C. (see Ching-I Peng, Clifford L. Schmidt, Peter C. Hoch & Peter H. Raven) 307

Houle, Gilles (see Ines Ben Mokhtar & Gilles Houle) 438

Hsu, Tsai-Wen (see Kuo-Hsiang Hung, Tsai-Wen Hsu, Barbara A. Schaal & Tzen-Yuh Chiang) 52

Hung, Kuo-Hsiang, Tsai-Wen Hsu, Barbara A. Schaal & Tzen-Yuh Chiang. Loss of Genetic Diversity and Erroneous Phylogeographical Inferences in *Lithocarpus konishii* (Fagaceae) of Taiwan Caused by the Chi-Chi Earthquake: Implications for Conservation 52

Jiménez, Juan A., Rosa M. Ros, María J. Cano & Juan Guerra. A Revision of *Didymodon* Section *Fallaces* (Musci, Pottiaceae) in Europe, North Africa, Macaronesia, and Southwest and Central Asia 225

Knapp, Sandra. Taxonomic Additions for *Solanum* Section *Geminata* (Solanaceae) in Peru 248

Koek-Noorman, Jifke (see Piero G. Delprete, Michael Nee & Jifke Koek-Noorman) 103

Küper, Wolfgang (see Colin J. McClean, Jon C. Lovett, Wolfgang Küper, Lee Hannah, Jan Henning Sommer, Wilhelm Barthlott, Mette Termansen, Gideon F. Smith, Simon Tokumine & James R. D. Taplin) 139

Leverich, Wesley J. (see Barbara A. Schaal & Wesley J. Leverich) 1

Li, De-Zhu (see Hong Wang & De-Zhu Li) 127

Linder, H. Peter (see Klaus Mummenhoff, Ihsan A. Al-Shehbaz, Freek T. Bakker, H. Peter Linder & Andreas Mühlhausen) 400

Lovett, Jon C. (see Colin J. McClean, Jon C. Lovett, Wolfgang Küper, Lee Hannah, Jan Henning Sommer, Wilhelm Barthlott, Mette Termansen, Gideon F. Smith, Simon Tokumine & James R. D. Taplin) 139

Lowry, Porter P., II (see Gregory M. Plunkett, Porter P. Lowry II, David G. Frodin & Jun Wen) 202

Manning, John C. (see Peter Goldblatt, John C. Manning & Peter Bernhardt) 268

Matthei, Oscar (see Víctor L. Finot, Paul M. Peterson, Fernando O. Zuloaga, Robert J. Soreng & Oscar Matthei) 533

McClean, Colin J., Jon C. Lovett, Wolfgang Küper, Lee Hannah, Jan Henning Sommer, Wilhelm Barthlott, Mette Termansen, Gideon F. Smith, Simon Tokumine & James R. D. Taplin. African Plant Diversity and Climate Change 139

McKenzie, R. J., J. Samuel, E. M. Muller, A. K. W. Skinner & N. P. Barker. Morphology of Cypselae in Subtribe Arctotidinae (Compositae–Arctotideae) and Its Taxonomic Implications 569

Miller, James S. (see Marc Gottschling, James S. Miller, Maximilian Weigend & Hartmut H. Hilger) 425

Mokhtar, Ines Ben & Gilles Houle. Photosynthate Contribution by Sepals Alleviates the Carbon Cost of Reproduction in the Spring Ephemeral *Floerkea proserpinacoides* (Limnanthaceae) 438

Morrone, Osvaldo, Sandra S. Aliscioni & Fernando O. Zuloaga. Análisis de la Diversidad y Distribución Geográfica de la Familia Poaceae en la Provincia de Jujuy, Argentina 595

Mühlhausen, Andreas (see Klaus Mummenhoff, Ihsan A. Al-Shehbaz, Freek T. Bakker, H. Peter Linder & Andreas Mühlhausen) 400

Muller, E. M. (see R. J. McKenzie, J. Samuel, E. M. Muller, A. K. W. Skinner & N. P. Barker) 569

Müller, Kai & Thomas Borsch. Phylogenetics of Amaranthaceae Based on *mat*K/*trn*K Sequence Data—Evidence from Parsimony, Likelihood, and Bayesian Analyses 66

Mummenhoff, Klaus, Ihsan A. Al-Shehbaz, Freek T. Bakker, H. Peter Linder & Andreas Mühlhausen. Phylogeny, Morphological Evolution, and Speciation of Endemic Brassicaceae Genera in the Cape Flora of Southern Africa 400

Murren, Courtney J. (see Michele R. Dudash, Courtney J. Murren & David E. Carr) 36

NEE, MICHAEL (see Piero G. Delprete, Michael Nee & Jifke Koek-Noorman) 103

NIE, ZE-LONG, JUN WEN, ZHI-JIAN GU, DAVID E. BOUFFORD & HANG SUN. Polyploidy in the Flora of the Hengduan Mountains Hotspot, Southwestern China 275

PENG, CHING-I, CLIFFORD L. SCHMIDT, PETER C. HOCH & PETER H. RAVEN. Systematics and Evolution of *Ludwigia* Section *Dantia* (Onagraceae) 307

PETERSON, PAUL M. (see Víctor L. Finot, Paul M. Peterson, Fernando O. Zuloaga, Robert J. Soreng & Oscar Matthei) 533

PHIPPS, J. B. A Review of Hybridization in North American Hawthorns—Another Look at "The *Crataegus* Problem" 113

PLUNKETT, GREGORY M., PORTER P. LOWRY II, DAVID G. FRODIN & JUN WEN. Phylogeny and Geography of *Schefflera*: Pervasive Polyphyly in the Largest Genus of Araliaceae 202

POTGIETER, C. J., & T. J. EDWARDS. The *Stenobasipteron wiedemanni* (Diptera, Nemestrinidae) Pollination Guild in Eastern Southern Africa 254

PURUGGANAN, MICHAEL D. & ROBERT H. ROBICHAUX. Adaptive Radiation and Regulatory Gene Evolution in the Hawaiian Silversword Alliance (Asteraceae) 28

RAVEN, PETER H. (see Ching-I Peng, Clifford L. Schmidt, Peter C. Hoch & Peter H. Raven) 307

ROBICHAUX, ROBERT H. (see Michael D. Purugganan & Robert H. Robichaux) 28

ROHWER, JENS G., & BARBARA RUDOLPH. Jumping Genera: The Phylogenetic Positions of *Cassytha*, *Hypodaphnis*, and *Neocinnamomum* (Lauraceae) Based on Different Analyses of *trn*K Intron Sequences 153

ROSENBAUM, HOWARD (see Paul Goldstein, Yael Wyner, Phaedra Doukakis, Mary G. Egan, George Amato, Howard Rosenbaum & Rob DeSalle) 12

ROS, ROSA M. (see Juan A. Jiménez, Rosa M. Ros, María J. Cano & Juan Guerra) 225

RUDOLPH, BARBARA (see Jens G. Rohwer & Barbara Rudolph) 153

SAMUEL, J. (see R. J. McKenzie, J. Samuel, E. M. Muller, A. K. W. Skinner & N. P. Barker) 569

SÁNCHEZ-ACEBO, LUPITA. A Phylogenetic Study of the New World *Cleome* (Brassicaceae, Cleomoideae) 179

SCHAAL, BARBARA A. & WESLEY J. LEVERICH. Conservation Genetics: Theory and Practice 1

SCHAAL, BARBARA A. (see Kuo-Hsiang Hung, Tsai-Wen Hsu, Barbara A. Schaal & Tzen-Yuh Chiang) 52

SCHMIDT, CLIFFORD L. (see Ching-I Peng, Clifford L. Schmidt, Peter C. Hoch & Peter H. Raven) 307

SKINNER, A. K. W. (see R. J. McKenzie, J. Samuel, E. M. Muller, A. K. W. Skinner & N. P. Barker) 569

SMITH, GIDEON F. (see Colin J. McClean, Jon C. Lovett, Wolfgang Küper, Lee Hannah, Jan Henning Sommer, Wilhelm Barthlott, Mette Termansen, Gideon F. Smith, Simon Tokumine & James R. D. Taplin) 139

SOMMER, JAN HENNING (see Colin J. McClean, Jon C. Lovett, Wolfgang Küper, Lee Hannah, Jan Henning Sommer, Wilhelm Barthlott, Mette Termansen, Gideon F. Smith, Simon Tokumine & James R. D. Taplin) 139

SORENG, ROBERT J. (see Víctor L. Finot, Paul M. Peterson, Fernando O. Zuloaga, Robert J. Soreng & Oscar Matthei) 533

SUN, HANG (see Ze-Long Nie, Jun Wen, Zhi-Jian Gu, David E. Boufford & Hang Sun) 275

TAPLIN, JAMES R. D. (see Colin J. McClean, Jon C. Lovett, Wolfgang Küper, Lee Hannah, Jan Henning Sommer, Wilhelm Barthlott, Mette Termansen, Gideon F. Smith, Simon Tokumine & James R. D. Taplin) 139

TAYLOR, CHARLOTTE M., ROY E. GEREAU & GRETCHEN M. WALTERS. Revision of *Ancistrocladus* Wall. (Ancistrocladaceae) 360

TERMANSEN, METTE (see Colin J. McClean, Jon C. Lovett, Wolfgang Küper, Lee Hannah, Jan Henning Sommer, Wilhelm Barthlott, Mette Termansen, Gideon F. Smith, Simon Tokumine & James R. D. Taplin) 139

TOKUMINE, SIMON (see Colin J. McClean, Jon C. Lovett, Wolfgang Küper, Lee Hannah, Jan Henning Sommer, Wilhelm Barthlott, Mette Termansen, Gideon F. Smith, Simon Tokumine & James R. D. Taplin) 139

WALTERS, GRETCHEN M. (see Charlotte M. Taylor, Roy E. Gereau & Gretchen M. Walters) 360

WANG, HONG & DE-ZHU LI. Pollination Biology of Four *Pedicularis* Species (Scrophulariaceae) in Northwestern Yunnan, China 127

WEIGEND, MAXIMILIAN (see Marc Gottschling, James S. Miller, Maximilian Weigend & Hartmut H. Hilger) 425

WEN, JUN (see Gregory M. Plunkett, Porter P. Lowry II, David G. Frodin & Jun Wen) 202

WEN, JUN (see Ze-Long Nie, Jun Wen, Zhi-Jian Gu, David E. Boufford & Hang Sun) 275

WYNER, YAEL (see Paul Goldstein, Yael Wyner, Phaedra Doukakis, Mary G. Egan, George Amato, Howard Rosenbaum & Rob DeSalle) 12

ZULOAGA, FERNANDO O. (see Víctor L. Finot, Paul M. Peterson, Fernando O. Zuloaga, Robert J. Soreng & Oscar Matthei) 533

ZULOAGA, FERNANDO O. (see Osvaldo Morrone, Sandra S. Aliscioni & Fernando O. Zuloaga) 595

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CONTENTS

A Review and Survey of Basicarpy, Geocarpy, and Amphicarpy in the African and Madagascan Flora ..... *Nigel P. Barker* 445

Revisión Sistemática del Subgénero *Harpostachys* de *Paspalum* (Poaceae: Panicoideae: Paniceae) ..... *Silvia Suyai Denham* 463

A Revision of *Trisetum* (Poaceae: Pooideae: Aveninae) in South America ..... *Víctor L. Finot, Paul M. Peterson, Fernando O. Zuloaga, Robert J. Soreng & Oscar Matthei* 533

Morphology of Cypselae in Subtribe Arctotidinae (Compositae–Arctotideae) and Its Taxonomic Implications ..... *R. J. McKenzie, J. Samuel, E. M. Muller, A. K. W. Skinner & N. P. Barker* 569

Análisis de la Diversidad y Distribución Geográfica de la Familia Poaceae en la Provincia de Jujuy, Argentina ..... *Osvaldo Morrone, Sandra S. Aliscioni y Fernando O. Zuloaga* 595

Checklist for authors 641

Index for Volume 92 645

Cover illustration. *Megacorax gracielanus* S. González & W. L. Wagner, first described as a new genus and species of the family Onagraceae from Mexico in *Novon* 12: 362, 2002. The generic name is based on the combination of the Greek words *mega*, large or great, and *korax*, raven, to honor Missouri Botanical Garden Director Peter H. Raven, author of numerous papers and monographs on many aspects of the family and one of our foremost advocates for conservation and sustainable use of the environment. The specific epithet honors Graciela Calderón Díaz-Barriga, major contributor to *Flora del Valle de México* and *Flora del Bajío* and mentor of several generations of students. The illustration is by Alice R. Tangerini (US).